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Dutch Carabidological Association

ECOLOGICAL CHARACTERIZATION OF CARABID SPECIES (COLEOPTERA, CARABIDAE) IN THE NETHERLANDS FROM THIRTY YEARS OF PITFALL SAMPLING

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An ecological characterization of 285 Dutch carabid species based on a large data set obtained by pitfall trapping in various habitats all over The Netherlands is presented. The data set contains ca. 1.5 million specimens, collected during thirty years in 1616 year-samples from 862 localities. Information about habitat, viz. type of vegetation, type of soil and humidity was recorded for each of the 862 sampling localities.

Two Way Indicator Species Analysis (TWINSPAN) as well as Detrended Correspondence Analysis (DECORANA) were used to classify the species into habitat groups. Seven principal habitat groups could be recognized. Indices for ecological amplitude, preference for soil type and humidity, are formulated and estimated for each species. This resulted in a description of the habitat preferences of the Dutch carabid species in far greater detail than was possible before. The classification is compared with others from the literature.

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In 1945, Lindroth published the first volume of his major work 'Die Fennoskandischen Carabidae' (Lindroth 1945). In this work he described the ecological preferences of the Fennoscandian carabid species. Since pitfall trapping was not practiced until about 1950, Lindroth's ecological characterizations were based on his own hand-collections, supplemented by those of other collectors, on laboratory experiments and on data taken from literature. This resulted in detailed descriptions of the species' ecological preferences. In 1949, Lindroth classified the species into a number of ecological groups, recognizing xerophilous species, mesophilous species (including ubiquists), hygrophilous species, arboreal species, forest species and synanthropous species (Lindroth 1949).

From about 1950 onwards, pitfall trapping became a commonly used technique in Europe. Thiele (1977) gave a summary of many ecological studies based on pitfall trapping carried out until ca. 1975. On basis of the results of these studies he characterized the carabid faunas of certain types of habitat, such as forests, sandy habitats and cultivated land, by presenting lists of characteristic species of these habitat categories. However, his tables only show the most abundant species in that particular habitat group giving no information about the occurrences of these 'typical' species in other types of habitat.

Luff et al. (1989) were the first to classify habitats of ground beetles based on a large data set from nearly 250 sites in North-East England. The carabid samples were grouped, based on presence/absence data, using the Two Way Indicator Species Analysis (TWINSPAN (Hill 1979a) and ordinated by Detrended Correspondence Analysis (DECORANA (Hill 1979b). Ten primary groups of carabid habitats were recognized, viz.: coastal, upland (dry, wet), woodland, grassland (dry, wet), riverside (boulders, shingle, sand) and marsh. Eyre & Luff (1990a) made a preliminary classification of European grassland habitats using carabids. The carabid assemblages of 363 pitfalled grasslands throughout Britain, were described by Eyre & Luff (1990b)

The characterizations of Lindroth (1945, 1949)

are usually considered to be accurate, although they were obtained with a non-quantitative method. Furthermore, Lindroths classification applies to the Fennoscandian situation, and species preferences may show geographical variation.

The major disadvantage of the analyses of Thiele (1977) is, that his compilations are based on data from the British Isles to Russia. Many of the species only occur in a limited part of this area.

The present study was carried out because there is a need for adequate ecological characterizations for the Dutch area with respect to future work, especially in the field of nature management and conservation. The material that is available from The Netherlands allows us to use quantitative methods to describe the ecological preferences of 285 species in our area in great detail. The ecological characterizations can serve as a basis for future descriptions and evaluations of carabid faunas of specific areas within The Netherlands.

MATERIAL AND METHODS

Material

When preparing the first edition of the Dutch carabid atlas (Turin, et al. 1977) it appeared that an enormous amount of data from pitfall trapping was available. Pitfalls were used in The Netherlands already in the early 1950's by Van der Drift, soon followed by Den Boer in 1953.

In the past, several studies concerning the efficiency of pitfall sampling have been carried out. A summary of the results of these investigations up to 1975 was published by Thiele (1977), concluding that pitfall trapping is a suitable technique for investigating carabid populations in a quantitative way. Den Boer (1977, 1990) reviewed investigations carried out by pitfall sampling at the Biological Station Wijster. It appeared that so-called year-catches of most carabid species give reliable relative estimates of the mean densities of active adult specimens around the pitfalls (Baars 1979, Den Boer 1979). A year-catch is defined as the summation per species of all specimens caught in one series of pitfalls during one year (or at least during the main reproductive period of carabids). These estimates are relative, meaning that they can be used only to compare the relative abundances within a certain species over a series of samples and/or years, but not between species. This is because each species has characteristic 'catch-parameters', such as activity pattern, way of living and catchability (see Luff 1975, Den Boer 1986).

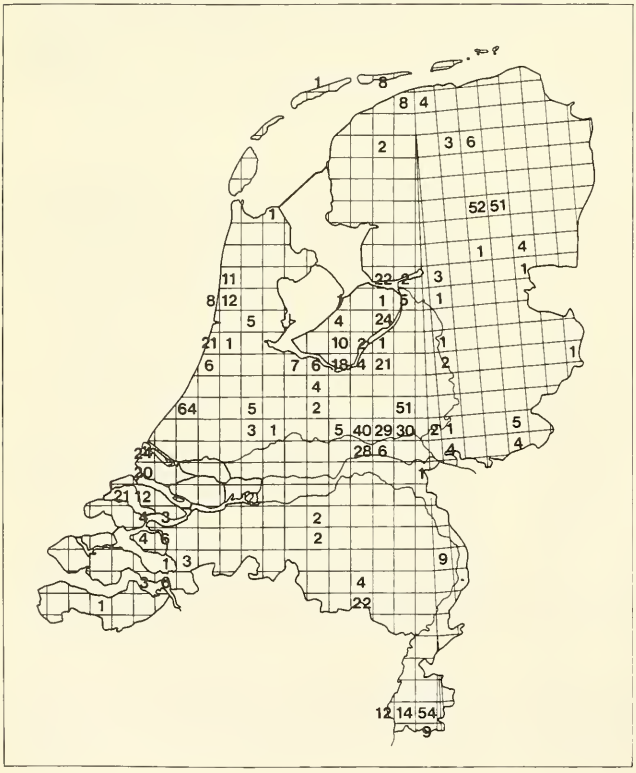


Fig 1. The number of sampled sites per 10 km square of the UTM-grid in the Netherlands.

The dataset for the present study consists of 1616 year-samples from 862 localities in The Netherlands (fig. 1), covering the period 1953-1983. A list of all year-samples included in the database is given by Turin & Penterman (1985).

The number of pitfalls used in a pitfall series and the sizes of the traps varied considerably between investigators. Therefore, the number of specimens in a year-sample were standardized by calculating the number of specimens per decimeter pitfall edge per year (SDY).

Before considering the catches, all sampling localities were uniformly described, using the 'eco-code' of the European Invertebrate Survey for The Netherlands (Van Tol 1979) in a slightly modified version (Penterman & Turin 1985). In this code information about type of vegetation, soil type, soil humidity, size of the locality and type of management is recorded. This information allowed us to recognize 33 habitats (table 1, p. 292), according to which the 1616 year-samples were coded.

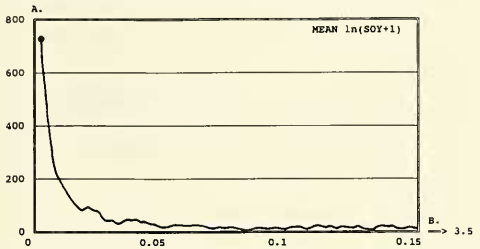


Fig. 2. The frequency distribution of the species mean ln(SDY+1)-values over each of the 33 habitats, taken from the data matrix. A: the Y-axis shows the number of relative abundances (see text) in the data matrix. B: the mean ln(SDY+1)-values; only a very small part of the X-axis is shown. This means that the values are very low all over the data matrix. These figures proved to be unworkable for TWINSPAN classification.

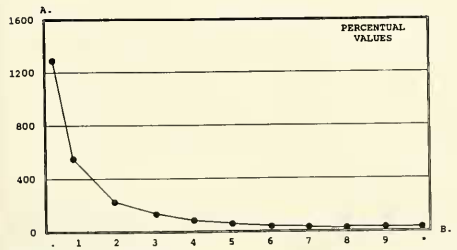


Fig. 3. The distribution of the pertage values after rescaling the mean abundances per species, with the maximum mean ln(SDY+1) put to 100% (relative occurrences). A: the Y-axis shows the number of relative occurrences. All figures from all 33 habitats are included except the first highest percentage value (* = 100%) of each species, which was used as a basic value for the rescaling. B: the percentage values, where: . = < 5%, 1 = 5-15%, 2 = 15-25% etc., 9 = 85-95% and * = > 95%; for further explanation see text and tables 2-9.

Classification of habitats and habitat preferences of species

Catches of a single carabid species from a large number of pitfall samples over many years, tend to form a log-normal distribution (Den Boer 1977). Therefore, the number of specimens per decimeter per year (SDY), was transformed to natural logarithms. For each of the 33 habitat categories (table 1) the mean value of ln(SDY+1) was calculated per species. Since all year-samples contribute to the mean ln(SDY+1) of a species, including those where the species was not recorded or in very low numbers only, the resulting values were very low for the majority of the species (fig. 2). Therefore, the values for the relative abundances were rescaled, by setting the highest value for a species at 100% and recalculating the SDY-values for the other habitats accordingly (fig. 3), in this way transforming the relative abundances into relative occurrences. This also made the catches of different species better comparable. We did not rescale the abundances of the species per habitat, in order to save the differences in significance between habitats as suitable sites for survival.

TWINSPAN was applied to the relative occurrences of the species, to classify the habitats into habitat groups and to obtain a classification of the species according to their habitat preferences based on the rescaled mean ln(SDY+1)-values. TWINSPAN was used using cut-levels 20, 40, 60 and 80% and was run several times using different pseudospecies' cut-levels. The results of these runs were all very similar when using the rescaled mean ln(SDY+1)-values. The results with different cut-levels based on the mean ln(SDY+1) values without rescaling, however, differed considerably among each other and were not further used. The resulting classification of habitats will be presented in the form of hierarchical tree diagrams and scattergrams. The full two-way table is presented, showing the group division of the species and containing the values indicating the relative occurrences as defined by the pseudospecies' cut levels. The information presented in this table allows us to easily evaluate the habitat specificity of a particular species.

Ecological amplitude

Two indices were defined and calculated that estimate the ecological amplitude of a species. The first measure (PRES) is based on the species presences over habitats, and is defined as:

$$PRES_j = \frac{n_j}{n}$$

where $PRES_j$ represents the ecological amplitude of the j-th species, n_j the number of habitats in which this species is present, and n the total number of habitats recognized (33). PRES will range from 0 to 1.

For the second 'eurytopy' estimate (SIM) the index of Simpson (D) is used (Simpson 1949), which characterizes the distribution of the abundances over the habitats in the form of: 1-D. This may thus be written as:

$$1 - \sum_{j=1}^{n} \left(\frac{a_j}{a_{tot}}\right)^2$$

where a_j is a measure of the relative abundance of a species in habitat group j and is equal to mean $\ln(SDY+1)_j$, while

$$a_{tot} = \sum_{j=1}^{n} \overline{\ln}\ (SDY + 1)_j$$

The value of SIM may range from 0 to 1.

Soil type and humidity

When characterizing the sampling localities, three humidity classes were recognized, viz. 'dry', 'moist' and 'wet'. The humidity preference of a species was estimated at an ordinal scale from 1 (very xerophilous) to 5 (very hygrophilous). Species only caught in 'wet' localities score 5, species from 'wet' as well as from 'moist' localities score 4, species only from 'moist' localities score 3, species from 'moist' as well as from 'dry' localities score 2 and species only from 'dry' localities score 1.

Each sampling locality was also classified into one of seven soil types: limestone (li), loam (lo), loamy sand/sandy clay (ls), river clay (rc), sea clay (sc), peat moor (pm) and sand (s). A species is regarded to show a preference for a certain kind of soil when the ln(SDY+1), averaged over all localities with this specific soil type, is at least 2 times the sum of the mean ln(SDY+1) values of the localities from the other soil types taken together.

Nomenclature and taxonomy

The nomenclature follows Turin (1990), except for three *Calathus* species of the *melanocephalus* group, for which is referred to Aukema (1990). The material from pitfall trapping presented here under the name of *C. melanocephalus* in fact is a mixture of *C. melanocephalus* and *C. cinctus* (Aukema 1990). Only in the more recent sampling (ca. after 1980), *C. cinctus* was recognized as a separate species. A similar problem exists where it concerns the species *Pterostichus nigrita* and *Asaphidion flavipes*. *Pterostichus rhaeticus* was not separated from *P. nigrita* (see: Koch 1984), and *Asaphidion curtum* as well as *A. stierlini* not from *A. flavipes* (see: Lohse 1983, Lompe 1989, Schweiger 1975). The full names of all species are given in the appendix.

RESULTS

Classification of habitats

Figs. 4-11 present the results from the TWINSPAN classification of the relative occurrences over the 33 habitats from table 1. Seven main habitat groups could be recognized (fig. 4):

Group I. – Peat and heath vegetations, habitats 1-5. A further subdivision of this end-group is presented in fig. 5.

Group II. – Poor grassland and dune habitats, habitats 6-11 (subdivision see fig. 6).

Group III. – Cultivated land and open coniferous plantations, habitats 12-15 (subdivision see fig. 7).

Group IV. – Mature forests, habitats 16-20 (subdivision see fig. 8).

Group V. – Moist/wet forests (forests in water meadows; brook forests) and ruderal grass localities, including limestone grassland, habitats 21-25 (subdivision see fig. 9).

Group VI. – Moist habitats overgrown with weeds, polder-(colonization-) habitats, habitats 26-30 (subdivision see fig. 10).

Group VII. – Wet habitats/shores, habitat 31-33 (subdivision see fig. 11).

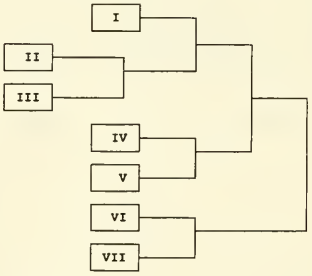
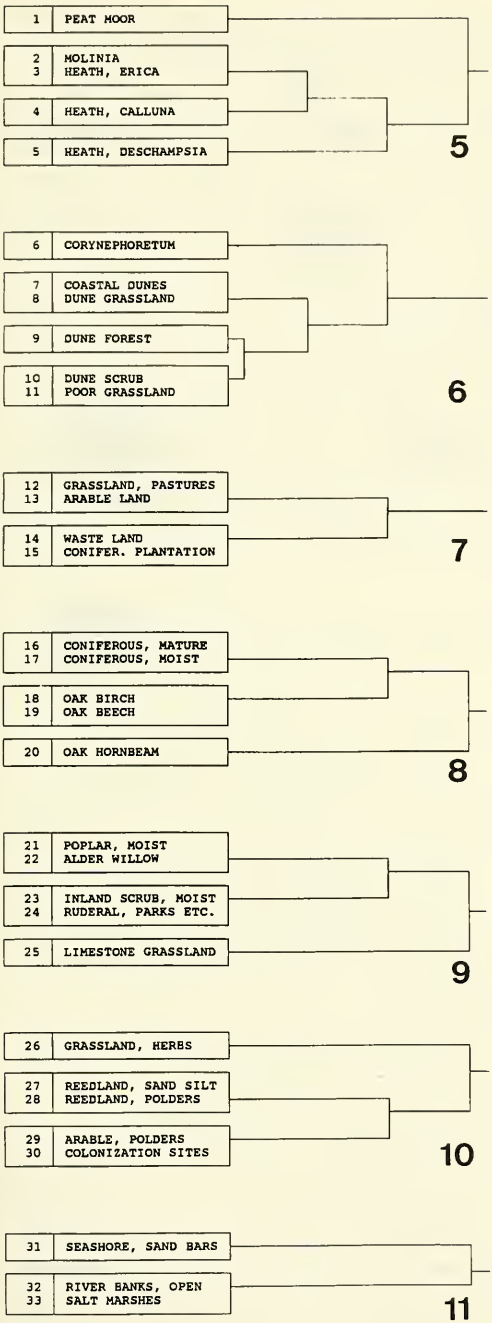


Fig. 4. Dendrogram of the main division into seven groups according to TWINSPAN classification of the species' relative occurrences. I-VII = main habitat groups: I = Peat and heathland vegetations (habitat 1-5, see fig. 5), II = Poor grassland and dune habitats (habitat 6-11, see fig. 6), III = Cultivated land and open coniferous plantations (habitat 12-15, see fig. 7), IV = Mature forests (habitat 16-20, see fig. 8), V = Moist / wet forests and ruderal grass localities, including limestone grassland (habitat 21-25, see fig. 9), VI = Moist habitats, overgrown with weeds, polder-(colonization-) sites (habitat 26-30, see fig. 10), VII = Wet habitats/shores (habitat 31-33, see fig. 11).



Figs. 5-11. Subdivision of habitat groups I-VII (see fig. 4 and table 1). – 5, group I; 6, group II; 7, group III; 8, group IV; 9, group V; 10, group VI; 11, group VII.

Fig. 12 shows the results of an ordination of the relative occurrences over the habitats by DECORANA, where the habitat groups mentioned above are indicated with dashed lines. The TWINSPAN divisions form rather coherent groups. The first axis of DECORANA is clearly correlated with moisture, dry habitats: 15-16, coniferous forest; 6, Corynephoretum; 4, Calluna-heath on the left, and wet: 31-33, shore habitats on the right. The second axis seems to be related in some way with the structure of the vegetation, open vegetations: 1-5, heath and peat habitats, 6-11, dune habitats in the lower part, and highly shaded vegetations: 16-22, forests in the upper part of the figure.

Classification of species

The habitat preferences of the species are indicated by their relative occurrences over the 33 habitats. The species are divided into eight species groups: A-H (fig. 13), and are tabulated in tables 2-9. Most groups contained very eurytopic as well as rare species. These species have been taken from the original groups and are brought together into two separate tables: 8 (eurytopic species) and 9 (rare species).

Species group A (table 2): Species of heath vegetations and peat moor, mainly occurring in habitat group I.

Species group B (table 3): Species of sandy localities, such as dunes, arable land and coniferous plantations; principal occurrences in habitat-group II and/or III.

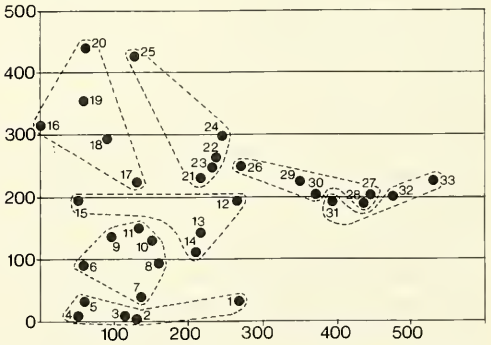


Fig. 12. Ordination by DECORANA, presenting on the first two axes the projections of the species scores for the 33 habitats (explanation see table 1). The dashed lines indicate the main habitat-groups: 1-5 = peat and heathland vegetations, 6-11 = poor grasslands and dune habitats, 12-15 = cultivated land and open coniferous plantations, 16-20 = mature forests, 21-25 = moist to wet forests and ruderal grassland habitats, including limestone grassland, 26-30 = moist habitats, reedland, pioneer (colonization-) habitats, polders, 31-33 = wet habitats, shores and river banks.

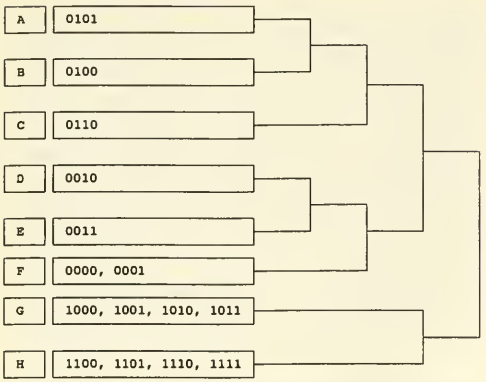


Fig. 13. Dendrogram of the species groups according to the TWINSPAN classification. The letters A-H indicate the TWINSPAN end-groups, treated in the respective species group. The numbers 0000-1111 indicate the first four levels of the TWINSPAN classification (compare table 2-7).

Species group C (table 4): Species of open areas, dune localities as well as colonization sites and shores, mainly in habitat-groups II, III and/or VI, VII.

Species group D (table 5): Species of forests and/or ruderal places, including limestone grassland; occurrences mainly in IV and/or V.

Species group E, F, G (table 6): These groups are not treated separately, because the separate end-groups are rather heterogeneous and less typical for a certain habitat group than the other species-groups. However, many species occur in moist and shaded localities, such as moist forests, scrubs and reedland; having an accent in habitat groups V and VI, and others show no special preference for moist habitats.

Species group H (table 7): Species of more open moist-wet habitats, reedland and shores; occurrences mainly in groups VI and/or VII, (TWINSPAN species end-groups 1100, 1101, 1110 and 1111).

Eurytopic species (EU) (table 8): These species are placed in a separate group on basis of their ecological amplitude: PRES $>$ 0.75 or SIM $>$ 0.85. The species are arranged according to their eurytopy estimates (Pres, Sim). The end-group number indicates from which of the species groups mentioned above (A-H) they originate.

Rare species (R) (table 9): Species have been placed in this group when the number of samples (Sa) $<$ 6 and when the number of individuals $<$ 50. If the species is merely present in 3-5 year-samples and these samples belong to the same habitat, the species was not placed into group H.

In tables 2-9 relative occurrences are presented according to the percentual scaling, where for each species the highest mean ln(SDY+1) in one of the 33 habitats, is put at 100%. In the body of the tables the numbers indicate: 1 = 5-15%; 2 = 15-25% etc., 9 = 85-95% and * = $>$ 95% respectively. Points indicate the habitats where the species is present, but where the relative occurrences are below 5%.

Species were ordinated by DECORANA, according to their relative occurrences per habitat. In figs. 14-20 the position of the species belonging to the groups A-H on the first two axes of the ordination is given. The first axis shows a dry-wet gradient: species preferring dry habitats (group A) on the left (fig. 14), and species from wet habitats (group H) on the right (fig. 19). The second axis is related with amount of shade: species of exposed habitats (group A) at the bottom (figs. 14, 15), and forest dwelling species (group D) at the top of the figure (fig. 17). The highly eurytopic species of group EU, take a central position according to that of the other species groups, resembling that of the intermediary groups E, F and G (fig. 18).

Ecological amplitude, soil type and humidity

The indices for the ecological amplitude of the species (Pres, Sim), for soil preference (So) and humidity preference (Hu) are given in the right columns of the tables 2-9. Also the number of year-samples (Sa), the number of individuals (N).

Discussion of the species groups

In this chapter we will give a short discussion per species group. Analyses more into detail can be expected in further papers where the species composition of several habitats or habitat-groups will be treated.

Species-group A (table 2 p. 294)

Most species listed in table 2 show clear preferences for peaty soils and/or sandy soils. When they have no preference for any soil type, they are mainly restricted to oligotrophic habitats. The humidity preference varies: most species that also occur in the Corynephoretum, such as *Pterostichus lepidus*, *Bradycellus ruficollis* and *Amara infima*, do not occur in humid habitats. Other species have a rather high preference for humid sites (humidity 4-5), such as *Pterostichus aterrimus*, *Agonum ericeti*, and *Anisodactylus nemorivagus*, which are known from literature as true peat-moor dwellers (Lindroth 1945, Mossakowski 1970a, 1970b). The results agree with those of investigations in German heath-moor complexes (Horion & Hoch 1954, Grossecappenberg et al. 1978). According to the TWINSPAN-classification (figs. 4-5), peat moor has

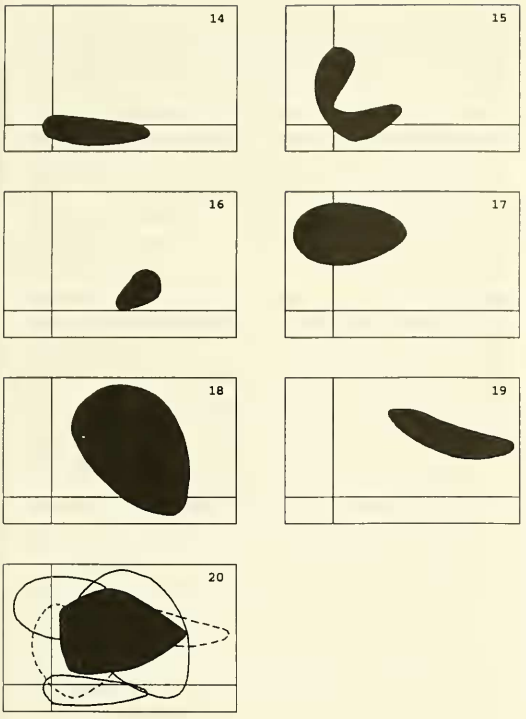


Fig. 14-20. Ordination of the species groups A-H and group EU, by DECORANA. – 14, group A: species of heath vegetations and peat moor (see table 2); 15, group B: species of sandy localities, dunes, arable land and coniferous plantations (see table 3); 16, group C: species of open areas (see table 4); 17, group D: forest species and species of ruderal places including limestone grasslands (see table 5); 18, groups E, F and G: species occurring in most and shaded habitats (see table 6); 19, group H: species of moist-wet habitats, reedland and shores (see table 7); 20, group EU: eurytopic species (see table 8); the outlines of the previous groups are indicated to accentuate the central position of the eurytopic species.

been included in the present species group and not in one of the moist groups E or F, in spite of the occurrence of many moist-preferring species. This can be explained by the fact that the fauna of peat-moor is rather poor in species and that the majority of these species is ecologically more related to heath-like vegetations. The peat-moor fauna has hardly any species in common with the carabid assemblages of shore habitats (species-group F), where the occurrence of many *Bembidion*-species is most characteristic. The results in table 2 agree well with those from the literature. Some studies carried out in Germany by Mossakowski (1970a, 1970b) and Rabeler (1947) also recognize *Agonum ericeti*, *Anisodactylus nemorivagus*, *Bradycellus ruficollis* and *Trichocellus cognatus* as characteristic species for peaty soil. Mossakowski (1964, 1970c) and Rabeler (1947) mention some species characteristic for heath vegetations, such as: *Amara infima*, *B. ruficollis*, *Carabus arvensis*, *C. nitens*, *Cicindela campestris*, *Olisthopus rotundatus* and *Pterostichus lepidus*. Some of the species mentioned by these authors can be found in the ecologically most related species group B (table 3) or they are arranged among the eurytopic or rare species (tables 8-9), e.g. *Bembidion nigricorne*, *Bradycellus caucasicus*, *Cicindela sylvatica*, *Pterostichus versicolor*, *Syntomus foveatus* as well as several *Calathus* and *Cymindis* species.

Species group B (table 3, p. 294)

This group is divided into two subgroups, based on a sixth level TWINSPAN division: B1 – species mainly occurring in the Corynephoretum, dune habitats and poor grassland; B2 – species of sandy arable land, waste land and young coniferous plantations on sand. The species of group B1 are in general confined to poor, dry and open, sandy habitats especially in dune areas. Some species are very stenotopic and more or less restricted to drifting sands of coastal and inland dunes: *Harpalus servus*, *Harpalus vernalis*, *Masoreus wetterhali*, *Ophonus cordatus* and *Harpalus neglectus*. Some papers concerning dunes and Corynephoretum sites (Schjøtz-Christensen 1957, 1966a, 1966b) mention several *Harpalus* species e.g.: *H. anxius*, *H. solitaris*, *H. neglectus* and *H. smaragdinus* as being typical for dry and sandy areas in Denmark. The following species can also be found in heath vegetations and they are obviously ecologically related to the species of group A: *Bembidion nigricorne*, *Cymindis macularis*, *Notiophilus germinyi* and *Cicindela sylvatica*. Most species in the B1 group have low humidity indices (1-2), and are rather stenotopic.

The species belonging to group B2 are characteristic for many types of sandy habitats. As far as they occur in cultivated areas, most of them avoid heavy fertilization. Species common to intensively cultivated agricultural land, can be found among the eurytopic species (see table 8). *Laemostenes terricola*, *Calathus micropterus* and *Pterostichus quadrifoveolatus* are also related to forests (habitat group IV).

Species group C (table 4, p. 295)

This small group consists of four species that occur primarily in open localities, dry as well as rather wet ones. *Clivina collaris* is predominantly a riparian species. The other species are confined to open country with a sparse vegetation and show a preference for coastal areas; this especially applies to *Calathus mollis*.

Species group D (table 5, p. 296)

Three subgroups were grouped together based on their occurrences in the main habitat groups IV and V: D1 – Stenotopic species of cultivated and ruderal sites such as poor unfertilized fields, gardens and limestone grasslands, mainly on limestone soil in the southern part of the province of Limburg; D2 – Species of more or less moist and shaded places partly on limestone soil; D3 – Eurytopic and stenotopic forest species.

Belonging to the first subgroup are several heath-preferring species (xerotherm species: Becker 1975, Lindroth 1949) which in The Netherlands are exclusively confined to limestone soil: *Parophonus maculicornis*, *Amara nitida*, *Brachinus crepitans*, *Harpalus dimidiatus*, and *Ophonus melleti*. Other thermophilous species can also be found on localities outside the limestone area of The Netherlands, on open sun-exposed, xerotherm sites such as slopes of river dikes with a southern exposition (Turin 1983, Turin et al. 1977): *Amara montivaga*, *Ophonus puncticeps*, *Harpalus rubripes*, and *Lebia chlorocephala*. *Ophonus rufibarbis* is the least thermophilous and most eurytopic *Ophonus* species. It can be found on more or less shady sites (Lindroth 1974, 1986).

The species of the D2 subgroup are restricted to the southern part of the province of Limburg or have a more or less fluviatile distribution in The Netherlands. Most species prefer chalky, clayish soil or loam, some of them inhabiting shaded (wooded) sites: *Stomis pumicatus*, *Bradycellus sharpi*, *Carabus coriaceus*, and *Pterostichus madidus*. These species also occur in limestone grassland at slopes with a northern exposition (Turin 1983).

Subgroup D3 consists of the true forest species. The first six species are rather eurytopic, which also applies to *Leistus rufomarginatus* and *Carabus problematicus*. Some of the more stenotopic forest species are more or less restricted to the oak-hornbeam forests of the southern part of Limburg and the easternmost part of The Netherlands, e.g. *Abax parallelus*, *Molops piceus*, and *Trichotichnus nitens*. *Amara praetermissa* can be found in the Corynephoretum, but also at acid sites on top of the limestone hills in Limburg with a more heather-like (*Calluna*) vegetation, which explains the presence of this species in the D-group.

There are far more investigations into the composition of the carabid fauna of forests than in that of heathland vegetations. Nowadays heathland is rapidly disappearing from The Netherlands, but about a hundred years ago it was one of the most prominent components of the landscape. In 1850 the area covered with forest was below 3%. Afforestation, which started in the first part of this century, has increased this area to about 6% in 1950 and 8-9% at the moment. Thus, many Dutch forests are rather young. The majority of this forested area consists of coniferous and exotic trees. Apart from the light oak-birch forests, which form the more natural climax vegetation on sandy soils, and the riverine forests, the more rich types of deciduous forest, e.g. Querco-Carpinetum, can only be found in restricted areas. Species characteristic (Thiele 1977) of these kind of forests in Central Europe, e.g. *Abax ovalis* (not in pitfalls), *Carabus auronitens*, *Molops piceus*, *Pterostichus cristatus* and *Trichotichnus nitens*, are restricted to the very eastern and southern parts of The Netherlands. Thiele (1977) reviews studies on the most abundant species of the (sub)centreuropic forests, including many investigations from Germany, such as those of Heckendorf et al. (1986), Kolbe (1968, 1970), Lauterbach (1964), Rabeler (1957, 1962, 1963, 1967 and 1969) and Thiele (1956). Also literature concerning The Netherlands was taken into account by Thiele, e.g. Van der Drift (1959) and Den Boer (1965). Recently, Turin & Heijerman (1988) carried out a first survey on the present data in a more simple way by only examining the species having the highest numbers of individuals and presences in all types of forest in The Netherlands together, and arranging them according to the fraction of specimens caught in forests, as compared with those in other habitats. The terms 'stenotopic / eurytopic forest species' they use, only apply to the Dutch area. Especially the species of mountainous localities are missing (highest altitude in The Netherlands is below 400 m). Most stenotopic forest species mentioned by Turin & Heijerman are now listed in table 5. Heijerman & Turin (1989) found great differences in fauna composition between forests in different parts of The Netherlands. This can possibly be explained by the fact that most of the forested areas are rather young and have been colonized recently.

Species group E, F, G (table 6, p. 297)

This group is polythetic and in fact a compilation of seven small TWINSPAN end-groups. The species predominantly occur in moist and shaded habitats. Most species are hygrophilous, reaching high numbers in wet grassy forests, moist grasslands and reedland: E1 – species of moist forests, sometimes in dune valleys and in moist grassland; F1 – two species of rather open and dynamic habitats; F2 – species of moist and shaded sites; G1 – only a single species; G2 – species with high numbers in reedland and in moist grassland, *Oodes helopioides* lives at wet and shaded sites; G3 – only *Bembidion obtusum*, which more or less prefers cultivated country; G4 – mainly hygrophilous spe-

cies of wet meadows, marshes and reedland. Most species in group G4 inhabit rather wet and dense, shaded vegetations. Exceptions are: *Amara ovata* and *A. famelica*, which both live in more open sites. Investigations into the fauna of moist and wet habitats are for reedland, swamps and lake shores: David & Marchal (1963), Dawson (1965), Jarmer (1971), Koch (1977), Obrtel (1972), Renkonen (1944) and Wasner (1977). The present results largely agree with the studies mentioned.

Species group H (table 7, p. 298)

The species belonging to group H reach high numbers in the moist or wet habitat groups VI and VII. Subdivisions based on the TWINSPAN classification are: H1 – a single rather eurytopic, colonizing species: *Amara similata*; H2 – mostly hygrophilous species of young habitats in polders and in other colonization sites; H3 – four species of open sites near water; H4 – Species of shore habitats, a number of them confined to saline localities. *Pterostichus cupreus* is similar to *Amara similata* in living in moist grassland and arable land, both species being rather eurytopic. *Bembidion bruxellense*, *Chlaenius nigricornis*, *Agonum albipes*, *Elaphrus cupreus* and *E. riparius* are characteristic of river meadows and reedland. *Amara convexiuscula* is a typical species of sea clay soil and found mostly along the coast, but it occurs, just as *Acupalpus exiguus*, *Lasiotrechus discus* and *Amara majuscula*, also in high numbers in the Dutch IJsselmeer polders (Turin et al. 1977). For large areas such as the Dutch polders, only constantly macropterous species and full-winged specimens of wing-dimorphic species are capable of colonizing such areas (Haeck 1971, Meijer 1973, 1974, 1980). In colonization of small sites, such as burnings and clearings, also big wingless species may be able to immigrate (Szyszko 1986), but in general, pioneer communities can be characterized by their high numbers of winged species. An example of long-term colonization and succession of carabids along rather homogenous road verges on clay soil in three Dutch polders of different age is given by Haeck et al. (1980). It illustrates that the carabid fauna of the Dutch polders keeps a coastal character for many decades.

Most species of the H4-group live close to water in open habitats. Several species of this group are restricted to the salt marshes of the Waddensea area and the islands of the province of Zeeland: *Dicheirotrichus gustavi*, *D. obsoletus*, *Pogonus chalceus*, *Bembidion normannum*, *B. pallidipenne*, *Dyschirius salinus*, *D. obscurus*, and *Bradycellus distinctus*. About saline habitats several studies are available: Heydemann (1962, 1967), Mossakowski (1971), Niemela (1988) and Rueda & Montes (1987) and they mention several species as typical for this habitat. The species occurring in saline habitats in The Netherlands are all treated in Turin (1991).

Many of the characteristic and abundant species of inland shores and river banks cannot be found in Group H, since pitfalls do not function well in shore habitats. Especially focused on the riparian fauna of running water are the studies of: Andersen (1970, 1982, 1983), Krogerus (1948), Lehmann (1965) and Plachter (1986). Species living so close to the water that they hardly can be trapped with pitfalls are for instance: *Agonum micans*, *Bembidion doris*, *B. obliquum*, *Dyschirius aeneus* and *Nebria livida*. The species *Bembidion articulatum*, *B. punctulatum*, *B. semipunctatum* and *B. testaceum*, all from river banks and often abundant in The Netherlands, are not present in the pitfall material. Some shore species that also can be found at some distance of the water, are listed among the rare species (table 9).

Eurytopic species (table 8, p. 299)

A group of 53 eurytopic species and ubiquists, extracted from all habitat groups on basis of their ecological amplitude. Most species in this group show high occurrences and abundances in one of the habitat groups III, V and/or VI. Apart from a few species, they do not clearly prefer a special soil type or humidity class. Some of them have high tolerances with respect to fertilizers and intensive agricultural management and can therefore be numerous in arable land and in pastures. Thiele (1977), who compared the carabid faunas of arable land, meadows / pastures and clover / alfalfa, in fact gives incomplete information of the species preferences. The species listed in Thiele's compilation are not characteristic for cultivated areas, but most of them simply are highly eurytopic species (see table 8). A similar survey was published by Basedow et al. (1976) and the results resemble those of Thiele.

Notiophilus biguttatus and *Nebria brevicollis* are eurytopic forest species that also occur in dense, shady grasslands and in other shaded sites, such as gardens and orchards (Turin & Heijerman 1988).

Rare species (table 9, p. 300-301)

A group of 59 rare species. Just as in the previous groups, the original TWINSPAN end-groups (GR) are mentioned after the species names. Twenty-six of the species only occur in one kind of habitat. For some species a lack of data is the main cause that the information on the species preferences is incomplete. However, for many species that have a highly restricted distribution in The Netherlands, especially those living near the fringes of their

ranges, the relative occurrences shown in table 9 will give a reliable picture of the species preferences in the Dutch territory. The species of this group will be treated in a separate study.

DISCUSSION

Only a few studies concerning classification of carabid species based on a large dataset are known from western and north-western Europe. The most important are chronologically: Lindroth (1945, 1949), Thiele (1977), Den Boer (1977), Luff et al. (1989) and Eyre & Luff (1990a, 1990b).

Lindroth (1945, 1949) indicated species preferences for humidity, and certain vegetation types, such as woodland. Although his conclusions were based mainly on material from Fennoscandia, his classification proved to be valuable for a much larger area. It was used in many carabidological studies all over northern and western Europe. When comparing the results of the present study with Lindroth's classification (table 10), one can conclude that they correlate rather well. The xerophilous species (X) in groups A1, B1, B2, C1 and D1 (table 10), the hygrophilous species (H) in groups A1, G4, H2, H3 and H4 (table 10) and the forest species (HW+W+WA) of Lindroth are found in groups D2, D3 and E1. Lindroth's mesophilous and more or less ubiquitous species (N) are scattered over a wide range of our species-groups with the highest numbers in the eurytopic EU-group (table 10). Fifty-nine species mentioned by Lindroth were caught in pitfalls in too low numbers for a characterization (group R) and 85 of the Dutch species mentioned by Lindroth, were not caught in pitfalls at all in The Netherlands (table 10 group O). From Lindroth's characterizations (table 10) we can conclude that these species that could not be characterized in the present study, belong to the inhabitants of shores and river banks (80 species, table 10). Others are very rare or even extinct in The Netherlands, e.g. many xerophilous species (see Desender & Turin 1989, Turin 1990).

Thiele (1977) attempted to characterize the carabid faunas of certain habitat groups such as forests, cultivated land and sandy habitats, comparing them on basis of species presence. He mainly used literature sources from the entire northwestern part of Europe. Although he included several lowland and mountain forests for the characterization of the forest fauna, we feel that this method gives an incorrect picture of the species preferences, especially because the relative occurrences and abundances in other localities were not taken into account.

Den Boer (1977) gives a far more complete picture for 75 of the most abundant species in his study area, by listing the data of hundreds of year-catches in many kinds of habitat in the province of Drenthe (The Netherlands). However, his study area is rather limited and many Dutch habitats and soil types are absent from his study (e. g. coastal dunes, clay soil and limestone grasslands). A comparison with Den Boer's results is not appropriate here, because his data form a significant part of our data set.

Several extensive studies on classification of carabid species have been published recently. Luff et al. (1989) is related to the classification of carabid habitats in north-east England, while another deals with the ground beetles of grassland habitats in Europe (Eyre & Luff 1990a). Finally, Eyre & Luff (1990b) presented a classification of ground beetles of the British grasslands in more detail. In all studies DECORANA and TWINSPAN were used as statistical methods. For the first study (Luff et al. 1989), very heterogenous material from 248 sites in North-East England was used, primarily collected for use in the British mapping scheme. Ten habitat groups were recognized based on the distribution of the species presence over the sites. A method was developed to fit in new sites. A first limitation of this method is that new sites can only be fit in using species that already contributed to the original ordination. Secondly, that only presence/absence data can be used. The original data set consists both of data from pitfalls, and sampling by hand. The possibility to include also samples from localities where pitfalls do not function, such as shore habitats, certainly is an advantage when using only the species presence. A main disadvantage is that the species' relative occurrences cannot be taken into account. The study of Luff et al. is, as they also notice in their discussion, in the first place a methodological one and the results do not give a definitive and complete picture of carabid habitats of the British Isles. Many habitats, for instance woodland, will have to be investigated more intensively. Three of the ten habitats do not occur in The Netherlands (upland dry, upland wet and boulder). The remaining habitat groups are rather broadly defined: coastal, woodland, dry grassland, wet grassland, wet running, wet still – silt, wet still – sand. It is rather difficult to compare the species preferences for British habitats with the present results, although many species preferences seem to correlate well, e.g. those of *Calathus erratus*, *Amara bifrons*, *Calathus rotundicollis* and those of many eurytopic species such as *Calathus melanocephalus*, *Loricera pilicornis*, *Pterostichus nigrita* and *Trechus obtusus*. From the present classification it can be learned that the most important environmental factor influencing the ordination of carabid species is soil moisture (fig. 14). This is in support of the

analyses by Luff et al. (1989). It is therefore very plausible that carabids are good indicators for moisture conditions in the field.

In the study concerning the heathland and grassland habitats in northern and central Europe, Eyre & Luff (1990a) used material from 638 heath and grassland pitfall sites. A number of these sites have also been used in the present study. Classification with TWINSPAN resulted in the identification of 17 habitat groups. In this study, woodland sites as well as shore habitats were not included. Although it is not easy to compare this classification with the present results, it is clear that some primary divisions are similar, e.g. heath, cultivated land and polders (pioneer habitat sites).

The classification of Eyre and Luff (1990b) concerns the classification of British grasslands. The data consist of material from all over England, Wales and Scotland. The results are to some extent supporting the present analysis. 'Dry' species, such as *Broscus cephalotes*, *Calathus mollis* and *C. fuscipes* are found in the same habitats in Britain. Also heath and peat-moor species (group A, table 2) have been placed in similar habitat groups in the analysis of Eyre & Luff. Some species that are recognized as woodland species in the present analysis, are scattered over many habitat groups in the British study. This is probably because mature woodlands have not been taken into account. In the results of both British studies (Eyre & Luff 1990b, Luff et al. 1989) some species preferences differ obviously from the situation in The Netherlands, e.g. the above mentioned species *Carabus violaceus*, *Pterostichus cristatus* and *P. madidus* seem to be much more eurytopic in England.

In their discussion Eyre and Luff (1990a) mention the scale problem, stating that the greater the area covered by a study, the less precise the results will be. It is obvious that in such a case the classification will be influenced by the geographical distribution of the species. A geographical component is even present within a relatively small study area as The Netherlands, where, for instance, *Pterostichus madidus* occurs only in the southern and central part of The Netherlands. The mean ln(SDY+1) in our method, however, is calculated over all samples of a certain habitat, also those situated outside the range of *P. madidus*. This problem applies to all species with a restricted distribution within a certain study area. The problem becomes more pressing, however, when the study area is still larger, because the relative number of species with restricted distributions will increase. On the other hand too small areas such as the province of Drenthe in The Netherlands (Den Boer 1977) contain not enough habitats to make a classification useful.

The present results will probably surprise experienced carabidologists to some extent. Several species show rather unexpected occurrences. *Abax parallelepipedus*, for instance, is a species characterized by many authors as restricted to forests, forest edges and hedges (Koch 1989, Lindroth 1986, Thiele 1977, Turin & Heijerman 1988), but appears to occur in a wide range of habitats abundantly, and in an even wider range in low numbers. It is a well known fact that species preferences for certain types of vegetation (habitats) can shift over geographical distance or at different altitudes. *Pterostichus cristatus*, for instance, is an inhabitant of cool mountain Fagetalia forest (Thiele 1977), but it also occurs in open, moist sites in Cumberland and Northumberland in the British Isles (Lindroth 1974). *Pterostichus madidus*, which inhabits the Fagetalia and Querco-Carpinetum (oak-hornbeam forest) (Koch 1989, Thiele 1977) in Central Europe, prefers open country and cultivated soil in the British Isles (Lindroth 1974, Eyre & Luff 1990a, Luff et al. 1989). In The Netherlands it takes an intermediate position (table 5). In the southern part of the province of Limburg *P. madidus* is the most abundant species in the forest edges of the oak-hornbeam forest, but it also occurs quite frequently and abundantly in shaded meadows and limestone grasslands without an extremely southern exposition. In the central part of The Netherlands it can only be found in light forest and in low numbers. The above mentioned differences between the present classification and that of British Isles will partly be due to such geographical differences in species habitat preferences.

We support the conclusion of Eyre & Luff (1990a) that classifications based on large datasets, together with the data from pitfall sampling from all over Europe, make carabid beetles a reliable group for environmental monitoring.

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Tables

Table 1. The 33 habitats recognized by the 'ecocode', and per habitat, the numbers of year-samples and the number of sites where pitfall series were situated.

NR	HABITAT	SAMPLES n	SITES n
1	Peat moor (wet, Sphagnum)	16	9
2	Heath with Molinia (moist)	28	9
3	Erica heath (moist)	14	7
4	Calluna heath (dry)	101	27
5	Heath with grasses, Deschampsia (dry)	119	26
6	Corynethoretum (dry, open)	65	24
7	Coastal dunes (dry, open)	53	20
8	Dune grassland (coastal)	69	29
9	Dune forest (coastal)	68	13
10	Dune scrub (coastal)	100	51
11	Poor grassland on sandy soil (inland)	23	14
12	Cultivated, pasture (inland, sand, fertilized)	33	22
13	Cultivated, arable (inland, sand, fertilized)	17	17
14	Cultivated, waste land (inland, sand)	26	11
15	Coniferous forest, plantation (open)	15	12
16	Coniferous forest, mature	65	64
17	Coniferous forest, old (moist)	11	11
18	Deciduous forest, oak-birch	126	73
19	Deciduous forest, oak-beech	41	34
20	Deciduous forest, oak-hornbeam	17	17
21	Deciduous forest, poplar (moist, polders)	19	13
22	Deciduous forest, alder-willow (moist-wet)	42	40
23	Inland scrub (moist)	44	22
24	Ruderal, park, orchard (dynamic)	40	40
25	Limestone grassland, dike slopes (xerotherm)	54	54
26	Grassland with herbs (inland, unfertilized)	98	70
27	Reedland, Lauwersmeer polder (sand-silt)	18	4
28	Reedland, IJsselmeer polder (sea clay)	52	22
29	Cultivated, IJsselmeer polder (sea clay)	52	26
30	Colonization sites, building lands (recent)	35	15
31	Sand banks near salt water, seashore (open)	93	40
32	Inland shores, river banks (open)	22	6
33	Salt marshes (sea clay)	40	20

Tables 2-9. The tables show the distribution of species relative occurrences over the 33 habitats recognized.

Explanation

A-H. – Tables 2-7, show the main species groups A-H, recognized by TWINSPAN classification. The sub-division of the main species-groups B and D is based on a sixth level, and those of groups E, F, G and H is based on a fourth level TWINSPAN division.

EU, RA. – The tables 8 and 9 show respectively the eurotopic (EU) and rare (RA) species, which have been separated from the main groups A-H. Eurytopic species (Pres $>$ 0.75 or Sim $>$ 0.85), have been placed into one group (table 8) to get a more clear picture of the most typical species of the principal groups A-H. The rare species have been separated from these groups for statistical reasons. They occur in too low numbers in The Netherlands (Sa $<$ 6 and N $<$ 50, except when all were found in the same habitat), to get a reliable picture of the species habitat preferences

NUM. – Species numbers. The full names with references to this number, can be found in the index

GR. – In tables 2-7 in this column the species group subdivision is indicated. In tables 8 and 9 the letters A-H refer to the original primary group where the eurytopic and rare species were placed by TWINSPAN classification

I-VII. – In the heading of the tables: main habitat groups that have been recognized by TWINSPAN classification (see fig. 4).

1-33. – In the heading of the tables: habitats, explanation see table 1.

1-9 and *. – In the body of the table, give relative occurrences according to the percentual rescaling per species (see text): '.' = ln(SDY+1) $\leq$ 5%, '1' = 5% $<$ ln(SDY+1) $\leq$ 15%, '2' = 15% $<$ ln(SDY+1) $\leq$ 25%, '3' = 25% $<$ ln(SDY+1) $\leq$ 35%, etc., '9' = 85% $\leq$ ln(SDY+1) $<$95%, '*' = 95% $\leq$ ln(SDY+1) $\leq$ 100% (This value stands for the ln(SDY+1) value that is put to 100%, which was the highest value of that species)

Pres. – Eurytopy estimation based on species presences: a low value means that the species is present in a low number of the 33 habitats; 1 means that the species is present in all habitats).

Sim. – Eurytopy measure based on the index of SIM D-1 (a low value means that the species is very stenotopic; highest value=0.94).

So. – Soil-preference measure, based on mean ln(SDY+1) figures; soil type / (all other soil types) $>$ 2, otherwise no indication of soil preference is given: c = riverclay + seaclay, li = limestone, ll = limestone + loam, lo = loam, ls = loamy sand / sandy clay, pm = peatmoor, rc = river clay, sa = sand, sc = sea clay, sm = sand + peatmoor.

Hu. – Humidity-preference measure (dry 456 samples, moist 690 samples, wet 461 samples), based on mean ln(SDY+1). 1 = mainly in dry samples [dry $>$ 10 $\times$ (moist+wet)], 2 = not in wet samples [dry+moist $>$ 20 $\times$ (wet)], 3 = not in dry and not in wet samples [moist $>$ 10 $\times$ (dry+wet)], 4 = not in dry samples [wet+moist $>$ 20 $\times$ (dry)], 5 = mainly in wet samples [wet $>$ 10 $\times$ (dry+moist)]

Sa. – Number of year-samples

N. – Number of specimens.

Table 2. Species of peaty soils and/or oligotrophic sandy soils.

Species group A1			I					II						III				IV					V					VI					VII						
NUM	Species	GR	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	Pres	Sim	So	Hu	Sa	N
1	Acupalpus dubius	A1		1	*	.																				4										.12	.48	pm	5	7	43
2	Pterostichus diligens	A1	4	*	3	4	6	.			.			.			.	.	.	.	.		.	1	1	.	.	1	.	1	.	1	.			.73	.83			418	16045
3	Carabus arvensis	A1	1	2	1	*	5	.						.	1			.	.	1	.				1		.	1								.45	.75	pm		164	1756
4	Pterostichus aterrimus	A1	*																	.	.															.09	.03	pm	5	4	87
5	Agonum ericeti	A1	8	1	8	*	1	.												.					.											.24	.70	pm		91	1199
6	Amara equestris	A1		.	.	*	*	.				.								.					.		.	.								.30	.55	sm		172	1859
7	Carabus nitens	A1	2	*	*	8	1	7												.					1				'							.24	.79	pm		75	286
8	Miscodera arctica	A1				*	8	2												2																.12	.65			14	24
9	Cymindis vaporariorum	A1		1	2	*	4	.									.											.								.21	.58	pm		99	282
10	Agonum versutum	A1	2	*	2			2																2												.15	.61	ls		6	19
11	Agonum krynickii	A1				*	*																													.06	.50	pm	4	6	9
12	Anisodactylus nemorivagus	A1			*																															.03	.00	pm	5	3	6
13	Olistophus rotundatus	A1		.	2	*	1	4					.		.		.		.	.					.	.										.36	.62	pm		115	727
14	Pterostichus lepidus	A1		1	1	*	7	4							1	1	5	.	.	.					.			.								.39	.80	pm		307	13284
15	Bradycellus ruficollis	A1	.	1	5	*	4	2				.	.				3		.	.					1		.	.			.		.			.55	.78	pm		275	5444
16	Carabus cancellatus	A1	6	4	3	6	1	*										.	2	1	.				1		.									.36	.83	pm		113	400
17	Notiophilus aesthuans	A1				*		2												2																.09	.39	pm		7	12
18	Trichocellus cognatus	A1	.	1	.	*	2	3									.			.					.			.								.30	.56	pm		180	3832
19	Harpalus latus	A1	.	4	2	4	*	.	.		.			2	.		4	.	1	.	.	.	.	.	2	.	1	1			.					.70	.84			313	6742
20	Harpalus solitaris	A1	.	.		9	*	2							.		*	.		.	.				1		.	.								.39	.75	sm		72	533
21	Cicindela campestris	A1	.	1	3	3	.	2					1		1		*											.								.30	.72	pm		73	154
22	Amara infima	A1		.		5	2	*									2																			.15	.60	sa	2	101	2055
23	Pterostichus minor	A1	*	1	.	.	.	.				.		.			.	.	.	.	.		.	2	1	1		.		1		2	.			.64	.70		4	120	963
24	Agonum sexpunctatum	A1	1	1	*	1	.	1					.	.	1	4	.		1	.			.		1			1	.	.	.	2	1			.64	.80			152	947

Table 3. Species of non-oligotrophic sandy soils with sparse vegetation. B1: species of *Corynephoretum*, dune habitats, and poor grassland. B2: species of sandy arable land and coniferous plantations.

Species group B1, B2			I					II						III				IV					V					VI					VII						
NUM	Species	GR	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	Pres	Sim	So	Hu	Sa	N
25	Calathus ambiguus	B1			.	.	.	*	8	3	.	3	.	.	1	5	3			.			.	.	.			.		.	.	.	6			.67	.84	sa		280	16294
26	Notiophilus substriatus	B1	2			.	.	1	.	1		1	1	6	.	*	.			.				.	.			1	.	.			1	.		.64	.77			80	146
27	Cicindela hybrida	B1				.	.	8	*	1		.					.							.	.								3			.30	.68		1	108	903
28	Demetrias monostigma	B1						1	*	2	.	1																					2			.18	.55	sa	1	14	36
29	Dromius spilotus	B1								1	*	1								3																.12	.53		2	10	15
30	Amara curta	B1					.	1	6	*	2	5	.		.					.			.	.		.	.	.							.	.45	.73	sa	2	257	2936

Table 3. (continued).

31	Panagaeus bipustulatus	B1						1	2	5	6	*	7							.			2	.	.	.	1									.36	.82	sa	2	161	457
32	Harpalus servus	B1				.	.	3	*	3	.	2	.		.		1		.									.						.		.39	.68	sa	1	203	4861
33	Harpalus vernalis	B1					.	1	3	*	1	4	.		1				1	.				1										.		.36	.73	sa	1	98	540
34	Harpalus xanthopus	B1					.	.	.	.	*	4	3		.					1							1	.						.		.36	.65	sa	2	123	881
35	Masoreus wetterhali	B1				.	1	9	9	*	.	1	7		.					.								.						.		.36	.78	sa	2	143	653
36	Bembidion nigricorne	B1		.	.	5	.	*						.			.			.	.															.27	.50	pm	2	103	5612
37	Cymindis macularis	B1				2	.	*									1			.					.											.18	.38	sa	1	69	712
38	Notiophilus germinyi	B1				1	1	*	2	2	1	1	.				3	.		.					.		.	.								.42	.74	sm	2	291	2507
39	Cymindis humeralis	B1				.		*									7	.																		.12	.51	sa	2	17	106
40	Amara lucida	B1						1	2	9	.	5		*					1									.					.			.27	.74	sa	2	105	559
41	Harpalus picipennis	B1								6		*	3										3													.12	.68		1	8	26
42	Amara eyrinota	B1								*		.																								.06	.03	sa	1	2	72
43	Ophonus cordatus	B1							*	1		.																								.09	.26	sa	1	13	49
44	Harpalus neglectus	B1					1	*	.	.		.	.																							.18	.26	sa	1	14	290
45	Cicindela sylvatica	B1				1	.	*																												.09	.25			14	24
46	Amara anthobia	B2						.				5	5	2		*				.				7	1											.24	.78	sa	2	21	256
47	Broscus cephalotes	B2	.	.		.	.	2	1	.		.		.	*	.	.		.	.				.	.	.		.				.	.			.61	.53		2	160	3413
48	Harpalus distinguendus	B2				.	.	.							1	*										.		.								.21	.25	sa	2	13	37
49	Laemostenus terricola	B2				.	.	4								1	*	1		.	.	2				.	.									.33	.67		2	43	381
50	Leistus spinibarbis	B2						3									*	1		.		.	.			.	.									.24	.49		2	34	676
51	Nebria salina	B2	.	.		1	.	2		.			1	.		*	4	.		.		.				.	.									.45	.63	sm		119	1355
52	Amara consularis	B2				.	.	.							7	*				.				.				.								.24	.51	sa	3	40	201
53	Amara fusca	B2													*																					.03	.00		3	9	29
54	Harpalus anxius	B2				1	1	*	.	1		.	1		4		2			.													.			.33	.70	sa	1	43	144
55	Harpalus smaragdinus	B2				.	.	.	.	.		.	1		7	*																	.		.	.33	.59	sa	2	33	201
56	Calathus cinctus	B2				.		1					.	1		*	1	.		.					.			.								.30	.42	sm	2	52	1186
57	Harpalus froehlichi	B2														*																				.03	.00	sa	3	5	19
58	Harpalus rufipalpis	B2		.		1	1	.					4	.		1	*	.	.	.	.				.		.	.								.45	.65	lo	2	101	895
59	Calathus micropterus	B2		.	1	.	1	.				.					*	2	1	.	1		.		.		.									.42	.59	sa	2	92	1553
60	Pterost. quadrifoveolatus	B2			1	.	.					.					*	1	1	.	.		.	.	.			.								.39	.38	sm		56	1553

Table 4. Species from open sites, that differ from those of the B-species.

Species group C1			I					II						III				IV					V					VI					VII								
NUM	Species	GR	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	Pres	Sim	So	Hu	Sa	N
61	Amara tibialis	C1				.	2	1		4		1	2		*	6				.										.	3	2		1		.39	.84			24	63
62	Clivina collaris	C1	3									.		3	*	3						2		.	1	1		5		.	1	2	.			.42	.84			44	143
63	Amara quenseli	C1						*									1															1	1	2		.15	.53			20	102
64	Amara fulva	C1				.	.	1		.		.	1	.	.	*				.			.	.	1			.		.	1	.	4	1	.	.61	.74			148	779
65	Calathus mollis	C1				.		.	5	2	.	5	.	.	1		1	.		.					.			.					*	1	.	.52	.76	sa		154	20441

Table 5. Species from shaded sites, either cultivated, ruderal or limestone grasslands (D1), moist shaded sites on chalky soil (D2), or forests (D3).

Species group D1-D3			I					II						III				IV					V					VI					VII						
NUM	Species	GR	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	Pres	Sim	So	Hu	Sa	N
66	Agonum gracile	D1	*			1				.		.								1			8		.			.								.24	.61	pm		15	28
67	Amara montivaga	D1																								6	*									.06	.47	li	2	7	83
68	Harpalus attenuatus	D1																								*										.03	.00	li	1	3	28
69	Ophonus puncticeps	D1										.														*	9	.				.				.15	.53	li	2	22	621
70	Harpalus rubripes	D1			.	.	.					1		.						.		1			3	*	5	.			1	.				.39	.69	li	2	50	691
71	Ophonus rufibarbis	D1									.	5		.						.				7	2	5	*	1								.27	.78	rc	2	25	135
72	Parophonus maculicornis	D1																								*		.								.06	.04	li	1	3	75
73	Bembidion gilvipes	D1																						6			*	1								.09	.53	rc	2	8	69
74	Amara nitida	D1																									*									.03	.00	lo	2	4	14
75	Brachinus crepitans	D1																									*									.03	.00	li	2	5	1831
76	Harpalus dimidiatus	D1																									*									.03	.00	li	2	4	6
77	Ophonus melleti	D1																									*									.03	.00	li	2	6	56
78	Lebia chlorocephala	D1																									*		.							.03	.00		2	4	4
79	Stomis pumicatus	D2													2		.	.		3	3		*	5	4	6	1	.		.	1	.				.42	.84			178	1737
80	Leistus fulvibarbis	D2										.							1	.	.	1		*	1		.	.				.				.30	.44			24	196
81	Epaphius secalis	D2																		*	.			6	*			1								.15	.67	rc	3	14	1063
82	Agonum livens	D2																		2	1		6	*												.12	.62	rc	4	6	19
83	Bradycellus sharpi	D2																		3			2	*			1									.12	.54	lo	4	6	43
84	Carabus coriaceus	D2																4		2		*		.	1	.	6	.								.24	.73	ll	2	55	703
85	Carabus monilis	D2										.		2						.		4	.	1	.	.	*	.								.30	.64	ll	2	77	1200
86	Pterostichus madidus	D2										.		.				.		.	.	*			.	1	4	.								.30	.50	ll	2	80	4117
87	Carabus auratus	D2																				4		.			*	.							.	.15	.47	li	2	55	2556
88	Cychrus caraboides	D3			1					.		.				I	5	*	1	3	4	.	5	1		.	.	.								.45	.83	lo	2	88	337
89	Notiophilus rufipes	D3			.	.	.	.	.		.	.	.			.	1	3	.	*	3	1	.		4	.	.	.								.61	.77			206	4319
90	Harpalus quadripunctatus	D3				.	.										1		1	*	4			.	3											.24	.65	pm	4	85	1779
91	Abax parallelepipedus	D3		.		.	.	.				.		.	.		4	7		2	4	*	.	.	1	.	1	.								.55	.80	ll		272	19720
92	Carabus violaceus	D3		.		.	1	.						.			.	4		2	5	*			1	3	3	.								.42	.81	ll	2	138	2097
93	Pterost. oblongopunctatus	D3		.	.	.	.	.						.	1	.	7	7	2	*	8	2	1	1	2	.	.	.				.				.64	.85			374	46040
94	Abax parallelus	D3																.		.	4	*			.		.									.18	.44	ll	3	47	1917
95	Molops piceus	D3																				*														.03	.00	lo	3	6	47
96	Trichotichnus nitens	D3																3		*		5														.09	.58	lo	2	8	129
97	Amara brunnea	D3				.	.	.				.		.			3	1	.	*	3				1			.								.36	.68	sa	2	73	3263
98	Amara pseudocommunis	D3				.		.												*																.09	.11	pm	4	29	146
99	Leistus rufomarginatus	D3				.	.	.			.	.				.	*	4	2	6	3	2	1	.	1	.		.			.					.55	.81			206	3451
100	Bembidion genei	D3													4							*			.											.09	.44	lo	3	6	63
101	Dromius agilis	D3	1														*	9	4	1																.15	.68	lo	2	21	28
102	Carabus problematicus	D3	.	.	1	1	2	1					.	.	.		8	*	1	3	1	.	.		3		.	.								.58	.82			361	15886
103	Amara praetermissa	D3						*				1								.					2		*	.								.18	.63	li	2	17	37

Table 6. Miscellaneous species, mainly of moist-wet, shaded sites (E1,F2), reedland (G2), marshes and wet meadows (G4) and related species (F1,G1,G3).

Species group E1, F1-F2, G1-G4		I					II						III				IV					V					VI					VII								
NUM Species	GR	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	Pres	Sim	So	Hu	Sa	N
104 Agonum viduum	E1	5									.							.				2	*	5	8		5								.24	.81			21	64
105 Acupalpus meridianus	E1							1	.	.										2			1	2	*					1	1				.27	.66	li		16	28
106 Badister unipustulatus	E1										1							1				4	*	3	5		3								.21	.79	pm		10	16
107 Badister meridionalis	E1										3	*					5					4	6			*	3								.21	.83	rc		13	24
108 Dromius quadrimaculatus	E1								2	5	5							2	3			4	*												.21	.81	rc		27	33
109 Amara bifrons	F1				.	.	.	.	8	.	1	1	.	1	1			.	.			.	.	3	*		.	I	1	.	.	5	2		.73	.83	rc		117	1083
110 Asaphidion pallipes	F1				1		2																	*	6	1	.				2	4			.24	.77	li	2	20	59
111 Trichocellus placidus	F2		I	.	.	.	.	.	.	.	.	.						1	4	3		*	2	3	.	.	.	.	2	.	5	.			.73	.83		257	5600	
112 Bradycellus verbasci	F2		.					.			.	.			1	1	.	.				7	5	8	1	.	1		3	1	*	.			.55	.84			103	868
113 Badister sodalis	F2	3																				1	*	5	*	4	8								.21	.81			37	151
114 Patrobus atrorufus	F2					.													1			1	6	2	*	.	2		.	.	3				.33	.75	rc	4	49	1004
115 Ophonus rupicola	G1							.					*													.						7			.12	.51		4	4	147
116 Acupalpus flavicollis	G2	*					.																				.		*	.	1				.18	.59	ls	5	15	79
117 Oodes helopioides	G2	*									.								.				.	1	1		1		5	.	.	.			.30	.63		4	29	251
118 Carabus granulatus	G2	*									.	.	3	1				.	.	.		.	5	2	.	.	6		5	1	2	.			.55	.84			131	1473
119 Bembidion obtusum	G3							.	.	.	.			1							.		.		*	.	.		.	.	1	5			.42	.59	li		54	574
120 Demetrias atricapillus	G4							2												6						2						*		4	.15	.71	ll		10	15
121 Omophron limbatum	G4										1													*			1		.			9	1		.18	.62	sa		8	159
122 Amara ovata	G4								2	1	2		2						2			2	3		1	1	6					*		2	.36	.84			21	74
123 Bembidion biguttatum	G4												2										5	2	4	1	*		1		4				.24	.78	rc		18	51
124 Bembidion dentelleum	G4												1										2	1	4	.	*			6	1	1	1		.30	.79	rc	4	13	233
125 Bembidion semipunctatum	G4																						*	2		1	8				*		4		.18	.78	rc		6	25
126 Pterostichus anthracinus	G4												1						.	.			5	1		.	*								.21	.58	sc		27	388
127 Bembidion harpaloides	G4										3												3	3			*		3						.15	.71	c		9	14
128 Elaphrus uliginosus	G4																							*			7		2						.09	.58	ls		6	10
129 Agonum moestum	G4	.		.	.	.	.										.		1	.	.	2	7	1	.	.	1	1	*	1	8	.			.61	.80	4		112	1195
130 Panagaeus cruxmajor	G4				1						1								.			1		.	8	3	.	*	*			.			.33	.76			33	71
131 Amara famelica	G4		3	.	3	1	.	.	.	.	.		.	1	.	.	.		.			.		.			.	.	2	.	*	2	.		.73	.78			163	1999

Table 7. Pioneer species of moist to wet habitats (H1-H3), including shore habitats (H4).

Species group H1-H4			I					II						III				IV					V					VI					VII						
NUM	Species	GR	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	Pres	Sim	So	Hu	Sa	N
132	Amara similata	H1				.	.	.		.				1	2	.			.	.	.	.	2	.	1	4	.	.		3	8	*	1			.64	.81	c		163	4047
133	Pterostichus cupreus	H2		.								.		1	3		.					.		1	.	.	.	2		1	*	2			.	.61	.73	sc		184	16261
134	Amara aulica	H2				.			.	.	.			.		1				.				.	.	1	1	1		.	2	*	1	.	.	.55	.67			60	318
135	Anisodactylus binotatus	H2	.	.	1	.	.	.					.	.		.			.	.	.		.	1	2	.		1	1	6	6	*	1			.67	.82			230	6660
136	Acupalpus exiguus	H2			.																			.	.			.		.	.	*	.			.24	.10	sc	4	22	674
137	Lasiotrechus discus	H2												.									1	2	1			1	1	3	7	*	1	.	.	.36	.76	sc		176	4537
138	Chlaenius nigricornis	H2	.	.		.	.										1			.	1				2		1	2		4		*		1		.39	.73			40	123
139	Bembidion bruxellense	H2	1	.		.		.				.		.	3							.			.			.		4	1	*	1	2	.	.52	.75			102	4516
140	Agonum albipes	H2											.	2						.				1	1			.	.	*		.	.			.30	.50	ls	4	30	913
141	Stenolophus mixtus	H2	1	.								.								.			.	.	2	.		.	.	8	3	*	2			.42	.74			124	35365
142	Amara majuscula	H2					.							.						.					.			.		3	2	*	.			.24	.54	sc		43	339
143	Nebria livida	H2																							.			.		1		*	.	1		.12	.35			8	27
144	Agonum thoreyi	H2	.						.			.											.		.	.		.	1	*	.	2	.	.		.39	.46	5		93	12062
145	Bembidion assimile	H2	1		.							.								.			.	.	1			.	5	*	1	6	1	.		.42	.74			148	22523
146	Bembidion fumigatum	H2																							.					*	.	1	.	.		.18	.27	sc		46	532
147	Bembidion iricolor	H2	.											.										.	.			.	2	*	2	2	.	1	.	.36	.62	sc	5	74	1260
148	Dyschirius luedersi	H2							.		.	.											.					.	*	1	.	.	.		.	.33	.26	ls		33	743
149	Elaphrus cupreus	H2	.			.	.	.						1						.				2	1	1		1		*		1	.			.39	.59	ls	5	38	1248
150	Bembidion lunulatum	H2												.						.			.	.	.			2	*	5	.	5	4	.	.	.42	.78		4	64	287
151	Elaphrus riparius	H2		.						.		.	1	.						.	.			.	1			1	.	*	.	*	7	2		.48	.77			66	1957
152	Acupalpus parvulus	H2	.	.		.	.	.				.								.			.		1	.	.	.	*	7	.	1	.	4		.55	.69	ls	5	116	1765
153	Bembidion femoratum	H3						.		.				.	2	.					.				1	.		.	.	1	.	1	*	1	.	.52	.58			121	25113
154	Amara convexiuscula	H3										.		.	.								.		.	.		.	1	3	1	5	*	1	1	.42	.74			142	6200
155	Bembidion quadrimaculatum	H3		.		.		.						.	2						.		.		.	2		1	.	1	*	3	3	2		.52	.80			97	1005
156	Dyschirius politus	H3						3	.	8		.																		*	2		2	5	4		.27	.81			29	128
157	Bembidion bipunctatum	H4																						.				.	*	8	.	2	8	1	.	.27	.72			101	11807
158	Agonum marginatum	H4		1	.	.	.	.	.			.	.	.					.	.			.	.	.			.	9	*	.	6	5	7	.	.67	.81	ls		139	1265
159	Bembidion aeneum	H4								.				.									.	.	.		.	.	*	1	.	.	1	7	1	.42	.65	ls	5	140	2565
160	Bembidion minimum	H4		.								.													.			.	7	3	.	.	2	*	5	.33	.74	ls	4	151	12934
161	Dicheirotrichus gustavi	H4										.													.			.	7	4		.	2	*	4	.24	.74	ls	5	140	62033
162	Dyschirius salinus	H4																							.			.	7	2			1	*	2	.18	.67	ls	5	110	17735
163	Dyschirius obscurus	H4																											2	3			*		1	.12	.53		5	40	2303
164	Bembidion varium	H4																					.	.	.		.		.	3	.	1	1	*	.	.36	.51	ls		105	12449
165	Dyschirius thoracicus	H4				.		1	.	.	.	.													1		.			2	.	1	*	1	1	.45	.60			129	23405
166	Bembidion argenteolum	H4							.																					3		.	*	6		.18	.62			30	883
167	Pogonus chalceus	H4												.														.	5	.			1	*	9	.21	.66	ls	5	98	8615
168	Bembidion normannum	H4												.														.	1	.			.	6	*	.21	.57		4	62	959
169	Pogonus luridipennis	H4																																*		.03	.00	ls	5	8	66
170	Bembidion velox	H4																														.	5	*		.09	.46	sa		5	186
171	Dicheirotrichus obsoletus	H4																														.	*		6	.12	.52	sc	4	51	931
172	Bradycellus distinctus	H4								.																							*			.06	.02	sa	4	18	192
173	Bembidion pallidipenne	H4																															*			.03	.00	sa	5	16	161

Table 8. Eurytopic species.

Eurytopic species, ubiquists, EU		I					II						III				IV					V					VI					VII						
NUMSpecies	GR	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	Pres	Sim	So	Hu	Sa	N
174 Agonum dorsale	H	.	.	.	.	.	.	.	.	.	.	.	2	1	1	.	.	.	.	.	.	.	.	1	.	1	.	.	.	*	1	.	.	.	.76	.69			311	16010
175 Harpalus tardus	B	.	.	.	.	.	.	.	1	.	1	2	.	2	*	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.79	.71		2	166	1506
176 Bembidion tetracolum	H	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	1	1	.	1	.	1	*	3	2	.	.	.79	.76			293	19171
177 Asaphidion flavipes	G	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	.	.	.	.	*	1	.	1	2	1	.	.	.	6	.	2	.	.	.79	.80			142	784
178 Pterostichus melanarius	H	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.	.	.	1	1	1	.	2	.	1	*	3	1	.	.	.97	.81			497	48335
179 Amara spreta	G	.	.	.	.	.	.	.	2	.	.	1	1	8	*	.	.	.	.	.	1	1	.	2	.	.	1	.	.	1	7	6	.	.	.85	.85			247	9930
180 Notiophilus aquaticus	A	.	1	4	*	2	5	.	1	1	1	.	.	1	4	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.85	.85	pm		397	13014
181 Bembidion guttula	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	*	4	2	1	4	2	1	2	4	.	.	.	.67	.85			107	403
182 Agonum assimile	D	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	*	6	2	1	8	3	4	.	1	.	.	.	1	.	.	.	.52	.85			118	3987
183 Syntomus truncatellus	B	.	.	.	.	.	1	1	4	*	8	5	3	.	1	4	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.70	.85	sa	2	302	3713
184 Calathus rotundicollis	D	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	3	*	8	7	7	5	1	2	.	.	.	.	.	.	.	.	.	.	.70	.85			231	6538
185 Pterostichus nigrita	G	*	2	2	1	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	1	3	1	.	.	.	.	9	2	3	1	.	.	.88	.86			429	8000
186 Bradycellus caucasicus	A	.	1	1	*	6	3	1	1	4	1	1	.	.	.	1	.	1	.	.	.	1	.	1	.	.	.	.	.	.	.	2	1	.	.64	.86	sm		284	1430
187 Carabus nemoralis	D	.	.	.	.	.	.	.	.	.	.	.	.	1	.	*	9	1	3	5	7	1	1	2	.	2	1	.	.	.	.	.	.	.	.67	.86			334	7396
188 Synuchus vivalis	E	.	.	1	.	.	.	.	.	.	.	1	2	7	1	.	.	.	.	.	.	1	1	2	*	2	1	.	.	3	.	.	.	.	.73	.86			108	377
189 Amara convexior	B	.	.	.	.	.	1	1	5	5	5	8	1	.	.	.	.	.	.	.	1	.	.	.	4	*	2	.	.	.	.	.	.	.	.70	.86		2	306	3625
190 Trechus obtusus	F	.	.	.	.	.	.	.	.	.	.	1	1	.	2	.	.	2	.	.	.	*	3	4	2	.	2	.	1	.	3	.	.	.	.82	.86			251	7930
191 Trechus quadristriatus	G	.	.	.	.	.	.	.	.	2	2	.	1	3	.	.	.	1	.	.	.	.	.	1	3	.	.	1	2	*	6	1	1	.	.76	.86			451	9616
192 Badister lacertosus	E	.	.	.	.	.	.	.	.	*	3	2	.	.	.	.	.	3	1	.	.	8	7	2	4	2	3	.	.	.	.	.	.	.	.36	.86			113	411
193 Amara lunicollis	A	2	8	1	5	*	1	.	.	.	.	2	1	1	.	2	1	1	.	.	.	.	.	1	.	1	4	.	.	.	.	.	.	.	.79	.87			545	50189
194 Pterostichus versicolor	A	.	4	3	*	8	1	.	.	.	.	.	2	.	1	4	.	.	.	.	.	.	.	2	.	.	5	.	.	.	.	.	.	.	.85	.87	sm		506	54592
195 Trechoblemus micros	G	.	.	.	.	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.	7	3	4	.	.	7	.	*	3	.	6	.	4	.27	.87			30	66
196 Dromius linearis	B	.	1	.	.	.	1	2	8	3	4	3	.	1	*	3	.	.	.	.	.	5	.	.	1	.	.	.	.	.	.	.	.	.	.48	.87		2	107	236
197 Leistus terminatus	E	.	1	1	2	.	1	.	.	.	1	.	.	.	1	3	1	8	3	.	.	9	*	3	.	.	1	.	.	.	2	.	.	.	.76	.87			230	931
198 Leistus ferrugineus	B	.	.	.	.	.	2	1	1	3	4	1	1	1	3	*	2	.	.	.	1	.	.	1	1	1	1	.	.	.	.	.	.	.	.79	.87		2	317	2049
199 Calathus erratus	B	.	.	.	4	2	*	5	4	.	2	2	.	*	1	9	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.88	.88	sm		620	54146
200 Amara familiaris	G	.	.	.	.	.	1	.	1	.	1	.	4	3	*	.	.	1	.	.	.	1	1	1	3	.	2	.	.	*	2	1	1	.	1.00	.88			372	3281
201 Amara apricaria	C	.	.	.	3	2	1	.	.	.	.	.	4	6	*	3	.	.	.	.	.	.	.	.	.	.	2	.	.	3	.	9	1	1	.76	.88			170	662
202 Syntomus foveatus	B	.	1	.	4	1	*	1	7	.	2	5	1	5	3	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.76	.88			364	3150
203 Agonum fuliginosum	F	3	4	.	1	.	.	.	.	.	.	.	.	.	1	.	.	4	4	.	.	1	3	1	.	.	.	1	4	.	*	.	.	.	.67	.88		4	168	690
204 Amara aenea	C	.	.	1	1	1	1	.	1	.	.	1	7	3	*	.	.	1	.	.	.	.	.	.	2	1	1	1	.	2	2	1	.	.	.97	.88			501	3541
205 Clivina fossor	H	.	.	.	.	1	.	.	.	.	.	.	2	.	2	.	.	.	.	.	.	5	2	2	.	.	3	*	2	8	2	1	7	.	.82	.88			461	4141
206 Dyschirius globosus	E	.	5	7	*	4	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	3	1	1	2	.	2	6	2	.	1	.	.	.	.88	.88			439	25073
207 Badister bullatus	E	.	.	.	.	.	.	1	2	5	7	4	1	.	.	.	.	1	1	.	.	5	4	2	*	1	2	.	.	1	.	.	.	.	.70	.89			227	687
208 Pterostichus strenuus	G	.	.	.	.	.	.	.	.	1	1	.	2	.	.	.	.	1	1	.	.	9	5	3	1	.	3	*	9	3	9	1	2	.	.91	.89			624	33119
209 Bembidion lampros	A	.	.	4	3	.	.	.	.	.	.	.	4	*	6	4	.	1	.	.	1	.	.	2	7	.	1	.	2	1	.	1	.	.	.91	.90			404	6530
210 Bradycellus harpalinus	A	.	1	1	*	4	3	.	.	.	.	1	.	1	8	4	.	.	.	.	.	5	.	2	.	.	1	2	1	.	1	1	1	.	.91	.90	sm		371	2612
211 Amara plebeja	G	.	.	1	1	1	1	.	.	.	.	.	2	2	*	.	.	.	1	1	.	1	.	2	.	.	1	3	4	5	7	1	.	.	.94	.90			459	6430
212 Agonum obscurum	E	.	4	1	6	3	.	.	.	.	.	.	.	2	.	2	1	7	1	.	.	9	4	4	1	.	1	.	.	.	*	.	.	.	.76	.90			393	14600
213 Harpalus affinis	E	.	.	.	1	1	.	.	.	.	1	2	5	8	8	.	.	.	.	.	.	1	.	1	*	1	3	2	.	4	2	4	1	1	.85	.90			343	3837
214 Notiophilus palustris	D	.	.	1	1	1	2	.	.	5	1	.	1	.	.	*	6	1	3	.	.	3	1	4	3	3	1	.	.	.	.	.	.	.	.79	.90			314	1327
215 Pterostichus vernalis	H	3	.	1	.	.	.	.	.	.	.	.	3	.	1	1	.	1	.	.	.	1	2	1	3	1	3	*	9	4	8	3	1	.	.97	.90			502	9221
216 Bembidion properans	H	.	.	.	.	.	.	.	1	.	.	.	*	4	2	.	.	.	.	.	.	.	.	.	2	1	3	9	5	8	7	8	4	2	.76	.90			256	3223
217 Dromius melanocephalus	B	1	3	.	1	7	1	1	4	2	5	*	.	.	9	7	.	5	.	.	.	1	1	1	.	.	1	.	.	.	.	.	.	.	.67	.90			118	230
218 Pterostichus niger	G	1	3	3	2	1	.	.	.	.	.	.	1	.	.	1	.	2	2	1	.	1	1	2	2	.	2	.	6	4	*	1	.	.	.88	.91			641	23117

Table 8. (continued).

219	Calathus melanocephalus	A	.	2	.	7	6	3	1	2	.	2	2	2	*	2	3	.	1	.	.	.	.	.	1	.	.	1	.	4	.	.	1.00	.91	sm		874	78250
220	Notiophilus biguttatus	D		.	.	.	.	.	.	.	2	1		.	1	.	7	5	7	*	8	5	*	2	4	3	1	.	.	.	1	.			.85	.91			446	7507
221	Agonum muelleri	G	.	.	1	.	.	1	.				.	9	.	3		1	1	1	.	2	6	1	1	5	5	5	.	5	6	*	1		.	.85	.91			225	725
222	Calathus fuscipes	B		.	1	1	2	6	2	*	1	4	9	7	*	7	8	.	3	1	.	.	.	1	1	.	3	2				.	1	.	.	.88	.92			575	23387
223	Harpalus rufipes	E	.	.	3	2	1	.	.	.	.	.	1	*	5	9	5	.	.	1	.	.	.	1	2	5	2	4	4	1	7	1	4	2	.	1.00	.93			532	5656
224	Loricera pilicornis	H	.	.	.	.	.	1	.	.	.	.	.	5	3	2	.	1	1	2	2	.	3	3	2	1	.	2	8	4	*	6	2	3	.	1.00	.93			685	7387
225	Amara communis	G	1	3	1	1	2	.	.	1	3	4	2	9	.	.	5	1	1	1	2	.	2	3	3	.	1	*	4	1	1	5	.	.	.	.97	.93			704	12776
226	Nebria brevicollis	E		.	3	1	1	1	.	1	.	1	2	7	2	3	*	1	5	4	4	7	3	6	4	4	2	2	.	.	5	2	1	.	.	.97	.94			665	30853

Table 9. Rare species

Rare species, RA			I					II						III				IV					V					VI					VII						
NUMSpecies		GR	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	Pres	Sim	So	Hu	Sa	N
227	Bembidion doris	A	*																	1																.06	.23		5	2	2
228	Carabus clathratus	A				*																														.03	.00		5	1	7
229	Cicindela germanica	A				*																														.03	.00			1	1
230	Agonum munsteri	A	*																																	.03	.00		5	1	1
231	Blethisa multipunctata	A	3	*																																.06	.35		5	4	7
232	Dromius angustus	B					4				*							7																		.09	.63		1	5	5
233	Microlestes minutulus	B						*				1															6									.09	.52	li	2	5	9
234	Harpalus luteicornis	B									7	*																								.06	.48		2	3	3
235	Harpalus serripes	B						*																												.03	.00		1	1	1
236	Harpalus melancholicus	B								*																										.03	.00		1	2	7
237	Harpalus flavescens	B											*																							.03	.00		1	1	2
238	Stenolophus teutonus	B	2													*																				.06	.26		4	2	2
239	Cicindela maritima	C							*			*																5					5			.12	.73		4	5	
240	Amara cursitans	D																								*										.03	.00	li	1	2	6
241	Bembidion deletum	D																								*										.03	.00	li	1	1	1
242	Dyschirius angustatus	D																								*										.03	.00	li	1	1	1
243	Tachys parvulus	D																								*										.03	.00	li	1	2	18
244	Bembidion quinquestriatum	D																							*											.03	.00	rc	3	1	1
245	Abax carinatus	D												3													*									.06	.37		5	2	7
246	Carabus convexus	D																									*									.03	.00	li	2	2	4
247	Ophonus puncticollis	D																									*						4			.06	.40	li	2	2	5
248	Lebia cruxminor	D																									*									.03	.00	li	1	1	1
249	Bembidion mannerheimi	D																			3				*	1										.09	.44	pm	5	3	29
250	Harpalus calceatus	D								2		1								2			*													.12	.49			5	7
251	Ophonus nitidulus	D																			*						6	2								.09	.56	li	2	4	4
252	Carabus auronitens	D																			*															.03	.00	sc	5	1	5
253	Pterostichus cristatus	D																			*															.06	.08	lo	3	2	9
254	Pterostichus macer	D																				*														.03	.00			1	1
255	Bembidion humerale	D																		*																.03	.00	pm	5	1	1
256	Calosoma inquisitor	D																*		1																.06	.11		3	2	6

Table 9. (continued).

257	Pterostichus gracilis	D										*								.03	.00		3	1	1
258	Dromius quadrisignatus	D								*										.03	.00		3	1	1
259	Harpalus honestus	D									*					2				.06	.24		1	2	2
260	Microlestes maurus	D									*					1				.09	.23		3	4	10
261	Amara strenua	D				8							*							.06	.49		1	3	4
262	Agonum micans	E												*		2				.06	.23	rc	3	2	23
263	Dromius sigma	E					*							9						.06	.50			2	2
264	Agonum piceum	F									*	2				5				.09	.53	ls	3	4	4
265	Badister dilatatus	F													*	3				.06	.38	pm	5	2	3
266	Bradycellus csikii	G			1	1	2									*				.15	.65			5	9
267	Ophonus azureus	G														8				.06	.50	li	3	2	2
268	Harpalus griseus	G										9				*				.06	.50		3	2	4
269	Badister peltatus	G	*													6			2	.09	.59		4	3	3
270	Trechus rubens	H													2		*			.06	.32	ls		3	6
271	Chlaenius vestitus	H						1								*		7		.09	.52	rc	5	3	7
272	Dyschirius aeneus	H														*		7		.06	.48	rc	5	2	6
273	Acupalpus consputus	H														*				.03	.00		5	1	5
274	Badister anomalus	H														*				.03	.00		3	1	2
275	Acupalpus brunnipes	H															*	3		.06	.34			3	7
276	Odacantha melanura	H	3														*	5		.09	.58	sc	4	5	8
277	Chlaenius tristis	H															*			.03	.00		5	1	1
278	Stenolophus skrimshiranus	H															*			.03	.00	sc	5	2	13
279	Bembidion lunatum	H				2											*			.06	.32			2	2
280	Bembidion quadripustulatum	H																*	4	.06	.40			2	2
281	Acupalpus elegans	H															*		6	.06	.46			2	2
282	Bembidion obliquum	H														1				.06	.13		5	2	2
283	Dyschirius nitidus	H																	.	.06	.07	sc	5	4	14
284	Bembidion laterale	H																	*	.03	.00		5	1	2
285	Dyschirius chalceus	H																	*	.03	.00		5	1	1

Table 10. A comparison between the classification made by Lindroth (1945, 1949, 1985 and 1986) for Fennoscandia and the present classification. The figures indicate the number of species that belong to the respective ecological groups. The columns A1-H4, EU, and RA in the heading of the table, refer to the species groups in the present classification (see tables 2-9), O = species common to Scandinavia and the Netherlands, but not present in the Dutch pitfall material. The rows in the table present the figures for the ecological groups of Lindroth: X = xerophilous species, N = ruderal and ubiquitous species, H = hygrophilous species; W = forest species and A = arborical species.

Group	A1	B1	B2	C1	D1	D2	D3	E1	F1	F2	G1	G2	G3	G4	H1	H2	H3	H4	EU	RA	O	Sum
X	12	17	12	3	9		2		1	1	1								12	15	19	104
NX			1		1	1													1		1	5
N	2	2			1			1					1	1	1	2	1		18	4	3	37
NH HW	1		1			2	1			1						2			8	1	1	18
H	7	1		1	2	1	1	1	1	1		3		11		16	3	17	7	31	49	153
HW	2					2	1	2		1									6	4	6	24
W WA		1	1			3	11	1											1	4	6	28
Sum	24	21	15	4	13	9	16	5	2	4	1	3	1	12	1	20	4	17	53	59	85	

Alphabetic list of species names with index to tables 2-9

Abbreviations: NUM = species number (table 2-9); So = soil preference; Hu = humidity preference; GR = species group; T = table number. For explanation see table 2-9, pp. 293-301.

Species	NUM	So	Hu	GR	T
Abax carinatus (Duftschmid)	245		5	RA	9
Abax parallelepipedus (Piller & Mitterpacher)	91	ll		D3	5
Abax parallelus (Duftschmid)	94	ll	3	D3	5
Acupalpus brunnipes (Sturm)	275			RA	9
Acupalpus consputus (Duftschmid)	273		5	RA	9
Acupalpus dubius Schilsky	1	pm	5	A1	2
Acupalpus elegans (Dejean)	281			RA	
Acupalpus exiguus (Dejean)	136	sc	4	H2	7
Acupalpus flavicollis (Sturm)	116	ls	5	G2	6
Acupalpus meridianus (L.)	105	li		E1	6
Acupalpus parvulus (Sturm)	152	ls	5	H2	7
Agonum albipes (F.)	140	ls	4	H2	7
Agonum assimile (Paykull)	182			EU	8
Agonum dorsale (Pontoppidan)	174			EU	8
Agonum ericeti (Panzer)	5	pm		A1	2
Agonum fuliginosum (Panzer)	203		2	EU	8
Agonum gracile (Gyllenhal)	66	pm		D1	5
Agonum krynickii (Sperk)	11	pm	4	A1	2
Agonum livens (Gyllenhal)	82	rc	4	D2	5
Agonum marginatum (L.)	158	ls		H4	7
Agonum micans (Nicolai)	262	rc	3	RA	9
Agonum moestum (Duftschmid)	129		4	G4	6
Agonum muelleri (Herbst)	221			EU	8
Agonum munsteri (Hellen)	230		5	RA	9
Agonum obscurum (Herbst)	212			EU	8
Agonum piceum (L.)	264	ls	3	RA	9
Agonum sexpunctatum (L.)	24			A1	2
Agonum thoreyi Dejean	144		5	H2	7
Agonum versutum Sturm	10	ls		A1	2
Agonum viduum (Panzer)	104			E1	6
Amara aenea (Degeer)	204			EU	8
Amara anthobia A. Villa & G.B. Villa	6	sa	2	B2	3
Amara apricaria (Paykull)	201			EU	8
Amara aulica (Panzer)	134			H2	7
Amara bifrons (Gyllenhal)	109	rc		F1	6
Amara brunnea (Gyllenhal)	97	sa	2	D3	5
Amara communis (Panzer)	225			EU	8
Amara consularis (Duftschmid)	52	sa	3	B2	3
Amara convexior Stephens	189		2	EU	8
Amara convexiuscula (Marsham)	154			H3	7
Amara cursitans (Zimmermann)	240	li	1	RA	9
Amara curta Dejean	30	sa	2	B1	3
Amara equestris (Duftschmid)	6	sm		A1	2
Amara eyrinota (Panzer)	42	sa	1	B1	3
Amara famelica Zimmermann	131			G4	6
Amara familiaris (Duftschmid)	200			EU	8
Amara fulva (Mueller)	64			C1	4
Amara fusca Dejean	53		3	B2	3
Amara infima (Duftschmid)	22	sa	2	A1	2
Amara lucida (Duftschmid)	40	sa	2	B1	3
Amara lunicollis Schioedte	193			EU	8
Amara majuscula Chaudoir	142	sc		H2	7
Amara montivaga Sturm	67	li	2	D1	5
Amara nitida Sturm	74	lo	2	D1	5
Amara ovata (F.)	122			G4	6
Amara plebeja (Gyllenhal)	211			EU	8
Amara praetermissa (C.R. Sahlberg)	103	li	2	D3	5
Amara pseudocommunis Burakowski	98	pm	4	D3	5
Amara quenseli (Schoenherr)	63			C1	4
Amara similata (Gyllenhal)	132	c		H1	7
Amara spreta Dejean	179			EU	8
Amara strenua Zimmermann	261		1	RA	9
Amara tibialis (Paykull)	61			C1	4
Anisodactylus binotatus (F.)	135			H2	7
Anisodactylus nemorivagus (Duftschmid)	12	pm	5	A1	2
Asaphidion flavipes (L.)	177			EU	8
Asaphidion pallipes (Duftschmid)	110	li	2	F1	6
Badister anomalus (Perris)	274		3	RA	9
Badister bullatus (Schrank)	207			EU	8
Badister dilatatus Chaudoir	265	pm	5	RA	9
Badister lacertosus Sturm	192			EU	8
Badister meridionalis Puel	107	rc		E1	6
Badister peltatus (Panzer)	269		4	RA	9
Badister sodalis (Duftschmid)	113			F2	6
Badister unipustulatus Bonelli	106	pm		E1	6
Bembidion aeneum Germar	159	ls	5	H4	7
Bembidion argenteolum Ahrens	166			H4	7
Bembidion assimile Gyllenhal	145			H2	7
Bembidion biguttatum (F.)	123	rc		G4	6
Bembidion bipunctatum (L.)	157			H4	7
Bembidion bruxellense Wesmael	139			H2	7
Bembidion deletum Serville	241	li	1	RA	9
Bembidion dentelleum (Thunberg)	124	rc	4	G4	6
Bembidion doris (Panzer)	227		5	RA	9
Bembidion femoratum Sturm	153			H3	7
Bembidion fumigatum (Duftschmid)	146	sc		H2	7
Bembidion genei Kuester	100	lo	3	D3	5
Bembidion gilvipes Sturm	73	rc	2	D1	5
Bembidion guttula (F.)	181			EU	8
Bembidion harpaloides Serville	127	c		G4	6
Bembidion humerale Sturm	255	pm	5	RA	9
Bembidion iricolor Bedel	147	sc	5	H2	7
Bembidion lampros (Herbst)	209			EU	8
Bembidion laterale (Samouelle)	284		5	RA	9
Bembidion lunatum (Duftschmid)	279			RA	9
Bembidion lunulatum (Fourcroy)	150		4	H2	7

Species	NUM	So	Hu	GR	T
Bembidion mannerheimi C.R. Sahlberg	249	pm	5	RA	9
Bembidion minimum (F.)	160	ls	4	H4	7
Bembidion nigricorne Gyllenhal	36	pm	2	B1	3
Bembidion normannum Dejean	168		4	H4	7
Bembidion obliquum Sturm	282		5	RA	9
Bembidion obtusum Serville	119	li		G3	6
Bembidion pallidipenne (Illiger)	173	sa	5	H4	7
Bembidion properans (Stephens)	216			EU	8
Bembidion quadrimaculatum (L.)	155			H3	7
Bembidion quadripustulatum Serville	280			RA	9
Bembidion quinquestriatum Gyllenhal	244	rc	3	RA	9
Bembidion semipunctatum (Donovan)	125	rc		G4	6
Bembidion tetracolum Say	176			EU	8
Bembidion varium (Olivier)	164	ls		H4	7
Bembidion velox (L.)	170	sa		H4	7
Blethisa multipunctata (L.)	231		5	RA	9
Brachinus crepitans (L.)	75	li	2	D1	5
Bradycellus caucasicus (Chaudoir)	186	sm		EU	8
Bradycellus csikii Laczo	266			RA	9
Bradycellus distinctus (Dejean)	172	sa	4	H4	7
Bradycellus harpalinus (Serville)	210	sm		EU	8
Bradycellus ruficollis (Stephens)	15	pm		A1	2
Bradycellus sharpi Joy	83	lo	4	D2	5
Bradycellus verbasci (Duftschmid)	112			F2	6
Broscus cephalotes (L.)	47		2	B2	3
Calathus ambiguus (Paykull)	25	sa		B1	3
Calathus cinctus Motschulsky	56	sm	2	B2	3
Calathus erratus (C.R. Sahlberg)	199	sm		EU	8
Calathus fuscipes (Goeze)	222			EU	8
Calathus melanocephalus (L.)	219	sm		EU	8
Calathus micropterus (Duftschmid)	59	sa	2	B2	3
Calathus mollis (Marsham)	65	sa		C1	4
Calathus rotundicollis Dejean	184			EU	8
Calosoma inquisitor (L.)	256		3	RA	9
Carabus arvensis Herbst	3	pm		A1	2
Carabus auratus L.	87	li	2	D2	5
Carabus auronitens F.	252	lo	5	RA	9
Carabus cancellatus Illiger	16	pm		A1	2
Carabus clathratus L.	228		5	RA	9
Carabus convexus F.	246	li	2	RA	9
Carabus coriaceus L.	84	ll	2	D2	5
Carabus granulatus L.	118			G2	6
Carabus monilis F.	85	ll	2	D2	5
Carabus nemoralis Mueller	187			EU	8
Carabus nitens L.	7	pm		A1	2
Carabus problematicus Herbst	102			D3	5
Carabus violaceus L.	92	ll	2	D3	5
Chlaenius nigricornis (F.)	138			H2	7
Chlaenius tristis (Schaller)	277		5	RA	9
Chlaenius vestitus (Paykull)	271	rc	5	RA	9
Cicindela campestris L.	21	pm		A1	2
Cicindela germanica L.	229			RA	9
Cicindela hybrida L.	27		1	B1	3
Cicindela maritima Latreille & Dejean	239			RA	9
Cicindela sylvatica L.	45			B1	3
Clivina collaris (Herbst)	62			C1	4
Clivina fossor (L.)	205			EU	8
Cychrus caraboides (L.)	88	lo	2	D3	5
Cymindis humeralis (Fourcroy)	39	sa	2	B1	3
Cymindis macularis Fischer von Waldheim	37	sa	1	B1	3
Cymindis vaporariorum (L.)	9	pm		A1	2
Demetrias atricapillus (L.)	120	li		G4	6
Demetrias monostigma Samouelle	28	sa	1	B1	3
Dicheirotrichus gustavi Crotch	161	ls	5	H4	7
Dicheirotrichus obsoletus (Dejean)	171	sc	4	H4	7
Dromius agilis (F.)	101	lo	2	D3	5
Dromius angustus Brulle	232		1	RA	9
Dromius linearis (Olivier)	196		2	EU	8
Dromius melanocephalus Dejean	217			EU	8
Dromius quadrimaculatus (L.)	108	rc		E1	6
Dromius quadrisignatus (Dejean)	258		3	RA	9
Dromius sigma (Rossi)	263			RA	9
Dromius spilotus (Illiger)	29		2	B1	3
Dyschirius aeneus (Dejean)	272	rc	5	RA	9
Dyschirius angustatus (Ahrens)	242	li	1	RA	9
Dyschirius chalceus Erichson	285		5	RA	9
Dyschirius globosus (Herbst)	206			EU	8
Dyschirius luedersi Wagner	148	ls		H2	7
Dyschirius nitidus (Dejean)	283	sc	5	RA	9
Dyschirius obscurus (Gyllenhal)	163		5	H4	7
Dyschirius politus (Dejean)	156			H3	7
Dyschirius salinus Schaum	162	ls	5	H4	7
Dyschirius thoracicus (Rossi)	165			H4	7
Elaphrus cupreus Duftschmid	149	ls	5	H2	7
Elaphrus riparius (L.)	151			H2	7
Elaphrus uliginosus F.	128	ls		G4	6
Epaphius secalis (Paykull)	81	rc	3	D2	5
Harpalus affinis (Schrank)	213			EU	8
Harpalus anxius (Duftschmid)	54	sa	1	B2	3
Harpalus attenuatus Stephens	68	li	1	D1	5
Harpalus calceatus (Duftschmid)	250			RA	9
Harpalus dimidiatus (Rossi)	76	li	2	D1	5
Harpalus distinguendus (Duftschmid)	48	sa	2	B2	3
Harpalus flavescens (Piller & Mitterpacher)	237		1	RA	9
Harpalus froehlichi Sturm	57	sa	3	B2	3
Harpalus griseus (Panzer)	268		3	RA	9
Harpalus honestus (Duftschmid)	259		1	RA	9
Harpalus latus (L.)	19			A1	2
Harpalus luteicornis (Duftschmid)	234		2	RA	9

Species	NUM	So	Hu	GR	T
Harpalus melancholicus Dejean	236		1	RA	9
Harpalus neglectus Serville	44	sa	1	B1	3
Harpalus picipennis (Duftschmid)	41		1	B1	3
Harpalus quadripunctatus Dejean	90	pm	4	D3	5
Harpalus rubripes (Duftschmid)	70	li	2	D1	5
Harpalus rufipalpis Sturm	58	lo	2	B2	3
Harpalus rufipes (Degeer)	223			EU	8
Harpalus serripes (Quensel)	235		1	RA	9
Harpalus servus (Duftschmid)	32	sa	1	B1	3
Harpalus smaragdinus (Duftschmid)	55	sa	2	B2	3
Harpalus solitaris Dejean	20	sm		A1	2
Harpalus tardus (Panzer)	175		2	EU	8
Harpalus vernalis (Duftschmid)	33	sa	1	B1	3
Harpalus xanthopus Gemminger & Harold	34	sa	2	B1	3
Laemostenus terricola (Herbst)	49		2	B2	3
Lasiotrechus discus (F.)	137	sc		H2	7
Lebia chlorocephala (Hoffmann)	78		2	D1	5
Lebia cruxminor (L.)	248	li	1	RA	9
Leistus ferrugineus (L.)	198		2	EU	8
Leistus fulvibarbis Dejean	80			D2	5
Leistus rufomarginatus (Duftschmid)	99			D3	5
Leistus spinibarbis (F.)	50		2	B2	3
Leistus terminatus (Hellwig)	197			EU	8
Loricera pilicornis (F.)	224			EU	8
Masoreus wetterhali (Gyllenhal)	35	sa	2	B1	3
Microlestes maurus (Sturm)	260		3	RA	9
Microlestes minutulus (Goeze)	233	li	2	RA	9
Miscodera arctica (Paykull)	8			A1	2
Molops piceus (Panzer)	95	lo	3	D3	5
Nebria brevicollis (F.)	226			EU	8
Nebria livida (L.)	143			H2	7
Nebria salina Fairmaire & Laboulbene	51	sm		B2	3
Notiophilus aesthuans (Motschulsky)	17	pm		A1	2
Notiophilus aquaticus (L.)	180	pm		EU	8
Notiophilus biguttatus (F.)	220			EU	8
Notiophilus germinyi Fauvel	38	sm	2	B1	3
Notiophilus palustris (Duftschmid)	214			EU	8
Notiophilus rufipes Curtis	89			D3	5
Notiophilus substriatus Waterhouse	26			B1	3
Odacantha melanura Paykull	276	sc	4	RA	9
Olistophus rotundatus (Paykull)	13	pm		A1	2
Omophron limbatum (F.)	121	sa		G4	6
Oodes helopioides (F.)	117		4	G2	6
Ophonus azureus (F.)	267	li	3	RA	9
Ophonus cordatus (Duftschmid)	43	sa	1	B1	3
Ophonus melleti Heer	77	li	2	D1	5
Ophonus nitidulus Stephens	251	li	2	RA	9
Ophonus puncticeps Stephens	69	li	2	D1	5
Ophonus puncticollis (Paykull)	247	li	2	RA	9
Ophonus rufibarbis (F.)	71	rc	2	D1	5
Ophonus rupicola Sturm	115		4	G1	6
Panagaeus bipustulatus (F.)	31	sa	2	B1	3
Panagaeus cruxmajor (L.)	130			G4	6
Parophonus maculicornis (Duftschmid)	72	li	1	D1	5
Patrobus atrorufus (Stroem)	114	rc	4	F2	6
Pogonus chalceus (Marsham)	167	ls	5	H4	7
Pogonus luridipennis (Germar)	169	ls	5	H4	7
Pterostichus anthracinus (Illiger)	126	sc		G4	6
Pterostichus aterrimus (Herbst)	4	pm	5	A1	2
Pterostichus cristatus (Dufour)	253	lo	3	RA	9
Pterostichus cupreus (L.)	133	sc		H2	7
Pterostichus diligens (Sturm)	2			A1	2
Pterostichus gracilis (Dejean)	257		3	RA	9
Pterostichus lepidus (Leske)	14	pm		A1	2
Pterostichus macer (Marsham)	254			RA	9
Pterostichus madidus (F.)	86	ll	2	D2	5
Pterostichus melanarius (Illiger)	178			EU	8
Pterostichus minor (Gyllenhal)	23		4	A1	2
Pterostichus niger (Schaller)	218			EU	8
Pterostichus nigrita (Paykull)	185			EU	8
Pterostichus oblongopunctatus (F.)	93			D3	5
Pterostichus quadrifoveolatus Letzner	60	sm		B2	3
Pterostichus strenuus (Panzer)	208			EU	8
Pterostichus vernalis (Panzer)	215			EU	8
Pterostichus versicolor (Sturm)	194	sm		EU	8
Stenolophus mixtus (Herbst)	141			H2	7
Stenolophus skrimshiranus Stephens	278	sc	5	RA	9
Stenolophus teutonus (Schrank)	238		4	RA	9
Stomis pumicatus (Panzer)	79			D2	5
Syntomus foveatus (Fourcroy)	202			EU	8
Syntomus truncatellus (L.)	183	sa	2	EU	8
Synuchus vivalis (Illiger)	188			EU	8
Tachys parvulus (Dejean)	243	li	1	RA	9
Trechoblemus micros (Herbst)	195			EU	8
Trechus obtusus Erichson	190			EU	8
Trechus quadristriatus (Schrank)	191			EU	8
Trechus rubens (F.)	270	ls		RA	9
Trichocellus cognatus (Gyllenhal)	18	pm		A1	2
Trichocellus placidus (Gyllenhal	111			F2	6
Trichotichnus nitens (Heer)	96	lo	2	D3	5